The Biology of Gordius robustus Leidy with a Host List

and Summary of the Public Health Importance of the Gordioidea

by

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ABSTRACT

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A classification and provisional key for species of the Gordioidea in California is presented, as well as a list of synonymies.

Examination of adult specimens of Gordius robustus Leidy by scanning electron microscopy (SEM) revealed that the technique is a useful tool for studying surface features. However, SEM was not considered to be a substitute for light microscopy.

The structure and development of the preparasitic stages of G. robustus have been carefully examined. For example, it was observed that larvae may hatch from eggs within 30-33 days at aquatic temperature of 68°F and pH 6.5; in 60-63 days at 50°F and pH 6.5; and no hatch resulted when the water was kept at 39.2°F and pH 6.5. No eclosion resulted when aquatic pH levels were 7

or higher, regardless of corresponding aquatic temperatures.

Newly-hatched preparasitic larvae of *G. robustus*, 106 to 150 µ in length, were observed to crawl by means of their proboscis and wriggling movements of the postseptum. Larval encystment either in or out of the water was not observed. Larvae survived approximately 3-5 days at 68°F, 5-6 days at 50°F, and subsequently died in a shrunken, contracted state.

Infectivity trials were successfully carried out by feeding *G. robustus* either as fully-differentiated larvae within their egg-shells or as newly-hatched preparasitic larvae to second-, third-, and fourth-stage larvae of *Aedes aegypti* (Linnaeus), *Aedes sierrensis* (Ludlow), *Culex pipiens* Linnaeus, and *Culex tarsalis* Coquillett. Gordian larvae, after penetrating their host's peritrophic membrane and mid-gut epithelial cells, moved into the hemocoel and frequently into other tissues, including muscles and hypodermis. Host melanization, as a defense reaction, frequently occurred within moments after gordian larvae entered the hemocoel of the immature mosquito host. Most of the parasites were killed as a direct result of encasement in melanin.

Field collections, at sites where mature specimens of *G. robustus* were recovered, yielded an aquatic damselfly nymph (Order Odonata) with three gordian larvae in its alimentary tract and two adult specimens of *Stenopelmatus longispina* Brunner, each of which had an adolescent specimen of the above gordian species in the hemocoel.

Drying was shown to be detrimental to larvae of G. robustus. All died when exposed for 20 seconds.

A survey of state and territorial health departments in the United States showed that hair-worms occasionally contaminate potable water supplies.

Studies on the tolerance of both mature and immature forms of G. robustus to chemical disinfectants in water indicate that the mature stage is quite resistant to residual levels of chlorine as commonly used in many water works.

A historical review of gordian host-parasite relationships is presented. Most of the literature on the subject pertains to parasitic associations with arthropods and other invertebrates. An extensive host list is presented, which cites specific associations between hair-worms and their respective hosts, including man and lower animals.

DEDICATION

This work is dedicated to my parents, Dario and Julie A. Cappucci, and brother, Dominic J. Cappucci, M.D., F.A.C.O.G., for their encouragement, loyalty, and devotion to high moral principles.

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SECTION 1

OUTLINE OF CLASSIFICATION AND PROVISIONAL KEY TO GORDIAN SPECIES IN CALIFORNIA

Introduction

At least seven species of gordian worms from California have been reported. Undoubtedly, with subsequent taxonomic revisions some hair-worm species with a geographic distribution that includes this state will be modified. However, a current classification and provisional key for species of the Gordioidea from California is still useful.

General Description of the Gordioidea

The body is long, filiform, unsegmented, and cylindric, approximately 10 to 70 cm. in length with a diameter of 0.3 to 3 mm. Males are usually smaller than females of the same species. Coloration is extremely varied and may be any shade of yellow, gray, tan, brown, or black. Depending on the species, the body surface may be spotted or stippled. Both extremities are more or less rounded without tapering. Oral and cloacal apertures are both terminal or subterminal, anteriorly and posteriorly respectively. The mouth may be

rudimentary or absent. The posterior end of the male's body often tends to coil ventrad.

Free-living, nonfeeding adults are frequently recovered from fresh waters or damp soils near the water edge. Immature gordiids are parasites in the body cavity of a number of insects and other arthropods, particularly crickets, grasshoppers, and terrestrial and aquatic beetles (Fig. 1).

The ranges of distribution for gordian worms in California most probably overlap the ranges of their hosts and are not very likely geographically restricted to one locality.

Classification for Gordian Species in California

Following is a classification for the different gordian worms recovered in California. The nomenclature of the subfamilies and higher categories is taken from Cheng (1973), Dorier (1965, 1970), and Grassé (1965).

Kingdom: Animalia Linnaeus, 1758.

Phylum: Nemathelminthes (Nematelmia Carl Vogt, 1851--Nemathelminthia Gegenbaur, 1859); Aschelminthes (Aschelminthia Grobben, 1910)

Class: Gordiacea von Siebold, 1843; Nematomorpha Vejdovsky, 1886

Order: Gordioidea Rauther, 1930

Family: Gordiidae May, 1919

Genus: <u>Gordius</u> Linnaeus, 1758

Species: <u>robustus</u> Leidy, 1851

Family: Chordodidae May 1919

Subfamily: Chordodinae Heinze, 1935

Genus: Neochordodes Carvalho, 1942

Species: occidentalis (Montgomery, 1898)

Subfamily: Parachordodinae Heinze, 1935

Genus: Gordionus Müller, 1926

Species: alpestris (Villot, 1884)

densareolatus (Montgomery, 1898)

longareolatus (Montgomery, 1898)

violaceus (Baird, 1853)

Subfamily: Paragordiinae Heinze, 1935

Genus: Paragordius Camerano, 1897

Species: varius (Leidy, 1851)

Key to Gordian Species in California

1. Posterior end of female with three caudal lobes that may be either parallel or divergent; cuticle with scattered areolae of one kind (Figs. 2, 3) .... Paragordius varius Leidy

   Posterior end blunt or bilobed; males and females 2

2. Posterior end of male bilobed and frequently with a tendency toward coiling.................................. 3

Posterior end blunt and without
caudal lobes; males and females 8

3. Postcloacal region of male with a crescent-shaped ridge; cuticle lacking areolae but may be marked with light-colored spots (Fig. 4)... <u>Gordius</u> <u>robustus</u> Leidy

Postcloacal region of male without a crescent-shaped ridge; areolae of one kind 4

4. Posterior end of male with long, slender caudal lobes 5

Posterior end of male with short, thick caudal lobes 7

5. Posterior end of male with two caudal lobes approximately two to three times as long as wide; lobes not armed with hairs or papillae (Fig. 5) .... <u>Paragordius</u> <u>varius</u> Leidy

Posterior end of male with two caudal lobes not over two times as long as wide; lobes armed with rows of long papillae on either side of the cloacal aperture 6

6. Areolae separated from each other by narrow [illegible]

interareolar structures such as granulations and pore canals; males (Fig. 6) .... <u>Gordionus</u> <u>alpestris</u> (Villot) *

Areolae separated from each other by conspicuously wide furrows containing interareolar structures such as granulations and pore canals; males (Fig. 7) ... <u>Gordionus</u> <u>violaceus</u> (Baird) *

7. Posterior end of male with two short, thick caudal lobes that are asymmetrical, divergent, and nearly conical; longitudinal axis of areolae nearly perpendicular to that of the body (Figs. 8, 9) .... <u>Gordionus</u> <u>densareolatus</u> (Montgomery)

Posterior end of male with two short, thick caudal lobes that are nearly parallel, terminally rounded, and more or less cylindrical; longitudinal axis of areolae parallel to that of the body (Figs. 10, 11) .... <u>Gordionus</u> <u>longareolatus</u> (Montgomery)

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*Males of these species have not been described from California.

8. Cuticle without areolae but may be marked with light-colored spots; females (Fig. 12) .... Gordius robustus Leidy

Cuticle with areolae of one kind .. 9

9. Cuticle with interareolar pore canals 10

Cuticle without interareolar pore canals 12

10. Areolae confluent or close together 11

Areolae separated from each other by conspicuously wide furrows; females (Fig. 13) .... Gordionus violaceus (Baird)

11. Areolae generally confluent, tending to produce transverse rows; females (Fig. 14) .... Gordionus densareolatus (Montgomery)

Areolae close together, separated by narrow furrows; females (Fig. 15) .... Gordionus alpestris (Villot)

12. Cloacal aperture of male elongate, situated approximately one body width from the posterior end of the body (Fig. 16) .... Neochordodes occidentalis (Montgomery)

Cloacal aperture of female
terminal, approximately mid-
centered, and circular in
outline (Fig. 17) .... Neochordodes occidentalis (Montgomery)

Addendum: Female specimens of Gordionus longareolatus (Montgomery) have not yet been described.

SECTION 2

LIST OF SPECIES SYNONYMIES OF THE GORDIOIDEA (GORDIAN WORMS) IN CALIFORNIA

Introduction

Information on the taxonomy and systematics of gordian worms is mainly European, as noted by the discussions and references in the reviews of Cheng (1973), Dorier (1965), Filipjev and Schuurmans Stekhoven (1941), Hyman (1951), Müller (1926), Pennak (1953), and Rauther (1930), and by the numerous citations in the annotated bibliography of Shephard (1974) and the index-catalogue of Stiles and Hassall (1920). The classification of gordiids from the New World is not well known (Pennak, 1953). However, valuable contributions have been made during the latter part of the nineteenth century and early portion of the twentieth century by Carvalho (1942), Leidy (1904), May (1919), and Montgomery (1898a, 1898b, 1903, 1904). Since the 1940's, only a meager amount of taxonomic information on gordian worms from the Western Hemisphere has been published, such as the works of Carvalho and Feio (1950), Cavalieri (1961), Faust and Botero Ramos (1960), León Varela and Garbarino (1962), Poinar and Doelman

(1974), and Scorza (1952). Currently, Redlich (1975) is in the process of preparing for publication the results and interpretations of studies on horsehair-worms from Canada.

On the following pages, a list of synonymies is presented on those species of hair-worms found in California. The synonymies are compiled without interpretive assertions, since opportunity to examine type specimens was limited. Some museums reported that they do not loan type specimens. A few museums noted that gordian worms originally deposited in their collections were either missing or destroyed. However, other museums circulated type specimens for observation and study. An alphabetical arrangement is followed to list the various synonyms. The most recent or the most commonly used scientific species name appears at the top of each synonymy, that is, <u>Gordionus alpestris</u> (Villot), <u>Gordionus densareolatus</u> (Montgomery), <u>Gordionus longareolatus</u> (Montgomery), <u>Gordionus violaceus</u> (Baird), <u>Gordius robustus</u> Leidy, <u>Neochordodes occidentalis</u> (Montgomery), and <u>Paragordius varius</u> (Leidy).

It is hoped that the presentation of the following synonymies will perhaps encourage others to reexamine the systematics and taxonomy of the gordian worms, since further studies are indeed warranted and essential.

Synonymy 1

Gordionus alpestris (Villot)

Gordionus alpestris Heinze, 1935c, pp. 661-662; 1937, pp. 296-298; 1941, pp. 38-39; 1952, p. 197. Dorier, 1946, p. 489; 1965, p. 1217. Mattes and Wignand, 1958, p. 302. Căpuse, 1970, p. 52.

Gordionus reticulatus Dorier, 1946, pp. 488-489.

Gordius alpestris Villot, 1884b, pp. 44-45. Guéguen, 1905a, pp. 257-266; 1905b, pp. 398-400. Stiles, 1907, p. 55. Stiles and Hassall, 1920, pp. 524-525.

Gordius reticulatus Villot, 1874, pp. 57-58, 67. Camerano, 1897a, p. 415. Montgomery, 1898a, pp. 26, 42-43. Stiles and Hassall, 1920, p. 533.

Gordius violaceus Baird, 1853a, pp. 36-37; 1853b, p. 20. Villot, 1886, p. 309. Römer, 1896, p. 266. Stiles and Hassall, 1920, p. 536.

Parachordodes alpestris Camerano, 1897a, p. 393. Stiles, 1907, p. 66. Stiles and Hassall, 1920, p. 640. Watson, 1960, p. 447. Faust et al., 1970, p. 406.

Synonymy 2

Gordionus densareolatus (Montgomery)

Gordionus densareolatus Heinze, 1935c, p. 662.

Gordius densareolatus Montgomery, 1898a, pp. 29, 33-34; 1898b, pp. 336, 339-340; 1899, pp. 650-652; 1907, p. 272. Stiles, 1907, p. 68. Ward, 1918, pp. 540-541. Stiles and Hassall, 1920, p. 527.

Parachordodes densareolatus Camerano, 1915, pp. 42-43.

Synonymy 3

Gordionus longareolatus (Montgomery)

Gordionus longareolatus Heinze, 1935c, p. 662.

Gordius longareolatus Montgomery, 1898b, pp. 334-335, 339-340; 1899, pp. 650-652; 1907, p. 272. Stiles, 1907, p. 68. Ward, 1918, p. 540. Stiles and Hassall, 1920, p. 530.

Parachordodes longareolatus Camerano, 1915, p. 43.

Synonymy 4

Gordionus violaceus (Baird)

Gordionus violaceus Müller, 1926, p. 199. Heinze, 1935a, p. 26; 1935c, p. 662; 1937, pp. 285-287; 1941, pp. 47-49. Mattes and Wignand, 1958, p. 302. Dorier, 1965, p. 1217.

Gordius violaceus Baird, 1853a, pp. 36-37; 1853b, p. 20. Montgomery, 1898a, pp. 42-43; 1907, p. 272. Topsent, 1900, pp. 86-91. Stiles and Hassall, 1920, p. 536. Vigueras, 1934, pp. 353-354.

Parachordodes violaceus Camerano, 1897a, pp. 392-393; 1915, pp. 44-45. Stiles, 1907, p. 66. Stiles and Hassall, 1920, p. 640. Watson, 1960, p. 447. Faust *et al.*, 1970, p. 406.

Paragordius violaceus Vigueras, 1934, pp. 353-354.

Synonymy 5

Gordius robustus Leidy

Gordius aeneus Villot, 1874, p. 52. Oerley, 1881, p. 329. Camerano, 1892a, p. 125; 1897a, p. 405. Römer, 1895b, p. 794; 1896, p. 268. Montgomery, 1898a, p. 27. Stiles and Hassall, 1920, p. 524. Carvalho, 1946b, p. 2. Sciacchitano, 1958, p. 97.

Gordius aquaticus Linnaeus, 1758, p. 647. Gmelin, 1790, pp. 3039, 3082. Dujardin, 1842, pp. 142-145. Leidy, 1856, p. 57; 1904, p. 105. Walsh and Riley, 1868, p. 57. Riley, 1870, p. 180. Villot, 1874, pp. 49-50. Römer, 1896, pp. 258-259. Montgomery, 1898b, pp. 335, 339-340; 1899, pp. 651-652; 1900, p. 95; 1907, p. 271. May, 1919, p. 138. Stiles and Hassall, 1920, pp. 525-526.

Gordius aquaticus var. *difficilis* Montgomery, 1898a, pp. 31-32; 1898b, pp. 339-340; 1899, pp. 651-652; 1907, p. 271. Stiles, 1907, pp. 67-68. Ward, 1918, p. 541. Stiles and Hassall, 1920, p. 526. Carvalho, 1946b, p. 2.

Gordius aquaticus var. *robustus* Montgomery, 1898a, pp. 30-31; 1898b, pp. 335, 339-340; 1899, pp. 651-652; 1900, p. 95; 1907, p. 271. Stiles, 1907, pp. 67-68. Stiles and Hassall, 1920, p. 526. Carvalho, 1946b, p. 2.

Gordius californicus Camerano, 1915, pp. 59-60. Carvalho, 1942, p. 217; 1946b, p. 2.

Gordius danielis Camerano, 1894, pp. 4-5; 1897a, p. 406. Montgomery, 1898a, p. 28. Stiles and Hassall, 1920, p. 527. Carvalho, 1942, p. 216; 1946b, p. 2.

Gordius guatemalensis Linstow, 1902, p. 228. Camerano, 1915, p. 55. Stiles and Hassall, 1920, p. 529. Carvalho, 1942, p. 217; 1946b, p. 2. Sciacchitano, 1958, p. 97.

Gordius lacustris Leidy, 1871, p. 307; 1904, p. 130. Montgomery, 1898a, p. 56 (of Leidy, a misprint for *G. robustus*). Stiles and Hassall, 1920, p. 530. Carvalho, 1946b, p. 2.

Gordius lineatus Leidy, 1851a, p. 263; 1904, p. 63. Montgomery, 1898a, p. 32; 1907, p. 271. Stiles and Hassall, 1920, p. 530.

Gordius longissimus Römer, 1895b, p. 796; 1896, pp. 272-273. Camerano, 1897a, p. 414. Stiles and Hassall, 1920, p. 531.

Gordius paranensis Camerano, 1892c, pp. 965-966; 1894, p. 4; 1897a, p. 406; 1901a, p. 1. Römer, 1896, pp. 270-271. Montgomery, 1898a, pp. 27, 40-41. Stiles and Hassall, 1920, p. 532. Carvalho, 1942, pp. 216-217, 1946b, p. 2.

Gordius robustus Leidy, 1851c, p. 275; 1856, p. 58; 1870, p. 194; 1879, pp. 10-11; 1904, pp. 65, 105, 153-154. Villot, 1874, pp. 51, 67. Riley *et al.*, 1878, p. 327. Stiles and Hassall, 1894, p. 351; 1920, p. 533. Montgomery, 1898a, pp. 26, 30, 32, 55-56. Camerano, 1903, p. 29; 1915, pp. 61-62. May, 1919, pp. 136-163. Pratt, p. 256. Caballero y Caballero, 1936, p. 481. Sayad *et al.*, 1936, pp. 461-462. Tanner, 1939, p. 2. Thorne, 1940, pp. 225-229. Carvalho, 1942, p. 217; 1946b, p. 2. Storer, 1943, p. 356. Woodhead, 1950, pp. 32-33. Baer, 1952, p. 43. Pennak, 1953, p. 235. Sciacchitano, 1958, pp. 97-98; 1963, p. 279. Wakeland, 1959, pp. 44-45. Beaver and Orihel, 1965, pp. 1014, 1017 (refer to Sayad *et al.*, 1936). Dorier, 1965, p. 1216. Faust *et al.*, 1970, p. 406. Storer *et al.*, 1972, p. 446. Cheng, 1973, p. 580. Rees, 1973, p. 90.

Gordius subspiralis Diesing, 1861, p. 601. Villot, 1874, pp. 51, 67. Camerano, 1895, p. 1; 1897a, p. 407; 1898, p. 75; 1915, p. 61. Montgomery, 1898a, pp. 26, 30. Stiles and Hassall, 1920, p. 534. Carvalho, 1946b, p. 2.

Gordius varius Leidy, 1870, p. 194. Montgomery, 1898a, pp. 55-56 (of Leidy, 1870)

Gordius villoti Rosa 1882, pp. 334-338. Montgomery, 1907, p. 271. Ward, 1918, pp. 540-541. May, 1919, pp. [illegible]. Stiles and Hassall, 1920, p. 536. Caballero y Caballero, 1936, pp. 479-481. Carvalho, 1946b, p. 2. La Rivers, 1949, p. 179.

Gordius willeyi Camerano, 1899, pp. 466-467; 1915, p. 62. Stiles and Hassall, 1920, p. 536. Carvalho, 1942, p. 217; 1946b, p. 2. Sciacchitano, 1958, p. 98.

Synonymy 6

Neochordodes occidentalis (Montgomery)

Chordodes gordioides Montgomery, 1898a, pp. 49-50; 1898b, pp. 336-338. Stiles and Hassall, 1920, p. 317.

Chordodes occidentalis Montgomery, 1898a, pp. 50-52; 1898b, pp. 336-340; 1899, pp. 651-652; 1900, p. 95; 1907, p. 272. Stiles, 1907, p. 68. Camerano, 1915, pp. 27-28. Ward, 1918, p. 538. Stiles and Hassall, 1920, p. 317. Pratt, 1935, p. 256. Caballero y Caballero, 1936, pp. 484-485.

Neochordodes occidentalis Poinar and Doelman, 1974, pp. 328, 330.

Synonymy 7

Paragordius varius (Leidy)

Chordodes varius Römer, 1896, pp. 279-280. Montgomery, 1898a, pp. 28, 45. Stiles and Hassall, 1920, p. 318. Carvalho, 1946b, p. 3.

Gordius aquaticus Linnaeus, 1758, p. 647. Gmelin, 1790, pp. 3039, 3082. Dujardin, 1842, pp. 142-145. Leidy, 1846, pp. 107-108; 1850, pp. 98-100; 1856, p. 56; 1878, p. 383; 1904, pp. 6, 33-36, 103, 150. Villot, 1874, pp. 49-50. Stiles and Hassall, 1920, pp. 525-526.

Gordius gratianopolensis Charvet of Schneider, 1866, p. 181. Montgomery, 1898a, p. 45. Stiles and Hassall, 1920, p. 529.

Gordius lineatus Leidy, 1870, p. 194. Carvalho, 1946b, p. 3.

Gordius longilobatus Leidy, 1870, p. 194. Riley et al., 1878, p. 327. Montgomery, 1898a, p. 55. Stiles and Hassall, 1920, p. 530. Carvalho, 1946b, p. 3.

Gordius tricuspidatus (Dufour, 1828) Meissner, 1856, p. 55. Siebold, 1856, p. 143. Leidy, 1856, pp. 56-57; 1904, pp. 103-104. Stiles and Hassall, 1920, p. 535.

Gordius bifurcatus White, 186[illegible], p. 175. Montgomery, 1898a, p. 55. Stiles and Hassall, 1920, p. 535. Carvalho, 1946b, p. 3.

Gordius trifurcatus-varius Stiles, 1907, p. 64. Stiles and Hassall, 1920, p. 535. Carvalho, 1946b, p. 3.

Gordius trilobus Villot, 1874, pp. 59, 67. Oerley, 1881, pp. 330-331. Camerano, 1897a, pp. 400, 414. Montgomery, 1898a, pp. 27, 45. Stiles and Hassall, 1920, p. 535. Carvalho, 1946b, p. 3. Dorier, 1946, pp. 480, 494.

Gordius varius Leidy, 1851a, pp. 262-263; 1851b, p. 266; 1856, pp. 56-57; 1858, p. 112; 1904, pp. 63-65, 103-105, 114. Diesing, 1861, p. 604. Riley, 1870, p. 180. Villot, 1874, pp. 59-60. Riley *et al.*, 1878, pp. 327, 329. Oerley, 1881, p. 331. Camerano, 1893, p. 216; 1895, pp. 5-6; 1897b, p. 3. Stiles and Hassall, 1894, p. 351; 1920, p. 535. Montgomery, 1898a, pp. 25, 28, 45. Carvalho, 1946b, p. 3.

Paragordius diversolobatus Heinze, 1935a, pp. 29-30. Carvalho, 1942, p. 216; 1946b, p. 3. Sciacchitano, 1958, p. 97.

Paragordius flavescens Linstow, 1906c, p. 246. Camerano, 1915, pp. 65-66. Stiles and Hassall, 1920, p. 641. Heinze, 1935a, pp. 27-29. Carvalho, 1942, p. 216. Sciacchitano, 1958, pp. 57-58, 97.

Paragordius tricuspidatus Camerano, 1897a, p. 400. Stiles and Hassall, 1920, p. 641. Dorier, 1930, p. 162. Bareth, 1974, pp. 658, 661.

Paragordius tricuspidatus var. *trilobus* Dorier, 1946, p. 494.

Paragordius trifurcatus = *varius* Stiles, 1907, p. 55 (= *varius*). Stiles and Hassall, 1920, p. 641.

Paragordius trilobus Dorier, 1946, pp. 493-494.

Paragordius varius Camerano, 1897a, p. 402; 1901b, p. 2; 1903, p. 26; 1915, p. 50. Montgomery, 1898a, pp. 45-47, 55-56; 1898b, pp. 336, 339; 1899, p. 651; 1903, pp. 387-474; 1904, pp. 738-755; 1907, p. 271. Ulrey, 1898, pp. 232-233. Stiles and Hassall, 1905, p. 127; 1920, p. 641. Stiles, 1907, pp. 59-64, 67. Ward, 1918, p. 539. May, 1919, pp. 164-175. Ackert and Wadley, 1921, p. 110. Vigueras, 1934, pp. 353-354. Pratt, 1935, p. 256. Caballero y Caballero, 1936, pp. 482-483. Tanner, 1939, p. 2. Carvalho, 1942, p. 214; 1946b, p. 3. Storer, 1943, pp. 355-356. Carvalho and Feio, 1950, pp. 204-205. Woodhead, 1950, pp. 32-33. Baer, 1952, p. 43. Scorza, 1952, pp. 50-52. Pennak, 1953, p. 235. Mattes and Wignand, 1958, p. 302. Sciacchitano, 1958, pp. 97-98. Watson, 1960, p. 447. Dorier, 1965, p. 1217. White, 1966, p. 579. Faust *et al.*, 1970, p. 406. Zapotosky, 1971, p. 228; 1974, p. 209; 1975, p. 103. Cheng, 1973, p. 580.

SECTION 3

ELECTRON SCAN OF THE CUTICULAR SURFACE OF *Gordius robustus* LEIDY

Introduction

The commercial application of scanning electron microscopy (SEM) in the biomedical and biological sciences has existed since the mid-1960's, and a vast amount of literature is now available describing the various principles, modes of operation, and techniques of SEM (Dawes, 1971; Glauert, 1972, 1974; Hayat, 1974a and b, 1975a and b, 1976; Johari, 1968-1970; Johari and Corvin, 1971-1975; Kay, 1966; Kessel and Shih, 1974; Koehler, 1973; Meek, 1970; Mercer and Birbeck, 1972; Thornton, 1968; Wells, 1974; Wischnitzer, 1970; and others). Basically, SEM provides surface information and not internal information as provided by light microscopy (LM) and transmission electron microscopy (TEM). The three types of microscopy can be used most effectively to complement each other (Port, 1975; Richards, 1974). SEM provides extreme depth of field, flexibility in contrast and brightness control, opportunity for interchanging high and low magnifications, and relatively great resolving power. It should be

realized that SEM is still somewhat costly and requires both specialized training and complex preparation of samples. Moreover, SEM is not a technique for routine laboratory analysis, but rather it is an investigative tool for diagnostic and morphologic studies (Port, 1975).

A number of citations on the usage of SEM in entomology and parasitology are available, including the reports of Baccetti and Capra (1970), Kessel and Shih (1974), Lumsden (1975), McKee (1973), Pease and Hayes (1968), Port (1975), Sher and Bell (1975), and Williams (1970). However, specific information on the application of SEM to examine the members of the Gordioidea, the gordiids or hair-worms, is very scant. Martin (1973) used SEM to examine the cuticular surfaces of male and female specimens of Chordodes sp. from Australia. Key morphologic features, such as areolae and body apertures, were readily discernible. In 1974, Eaken and Bradenburger reported that they briefly utilized SEM in conjunction with more extensive TEM studies to examine the ultrastructural morphology of gordian worms. Descriptions of surface observations by SEM were quite limited and did not include information about taxonomic characters, such as the worms' anterior and posterior extremities. More recently, Redlich (1975) has been using SEM in taxonomic studies on hair-worms from the Pacific Northwest.

Related information on the use of TEM to examine gordian ultrastructure has appeared in the reports of Bresciani (1970), Nicholas (1970), and Zapotosky (1971, 1974, and 1975). In addition, recent studies with LM to elucidate the morphology and taxonomy of gordiids have been documented by Bareth (1974), Inoue (1972, 1974),

Poinar and Doelman (1974), Reutter (1972), Yokoyama and Inoue (1971), and others.

The purpose of this study was to examine male and female adult specimens of *Gordius robustus* Leidy by the SEM technique and to evaluate the usefulness of SEM in the study of gordian worms.

Materials and Methods

The adult hair-worms used in this study, five males and five females, were collected by the author in 1974-75 from fresh-water sources in Contra Costa, Mendocino, Santa Clara, Solano, and Yolo Counties in Northern California. The identity of the worms was determined by LM to be *G. robustus* (see Figs. 18, 19 and provisional key to gordian species in California).

Since the methods of preparing biological specimens and subsequent modes of operation in SEM are still somewhat individualized, and not yet generalized, details are given of the various steps in fixing, drying, and coating samples. The intact worms were initially washed for a few minutes by gentle agitation in distilled water to remove extraneous debris from the cuticle and thus avoid as much as possible any surface distortions that may hinder later SEM observations and interpretations. Both anterior and posterior extremities, approximately one-half to one-third inch in length, were removed from the body of each worm and saved for further processing. Some mid-body sections, also about one-half to one-third inch in length, were included in the dissected material retained for later examination.

The specimens were prefixed at 35°F for one hour in 2-per cent glutaraldehyde buffered with 0.1M phosphate buffer solution, then

washed for two minutes in 0.1M phosphate buffer solution, and later fixed in one-per cent osmium in phosphate buffer solution (pH 7.2) for one hour at 35°F. Again, the samples were washed for two minutes in 0.1M phosphate buffer solution. Initial dehydration of the samples was accomplished via immersion for 20 minutes in each of six different concentrations of ethanol (20-per cent, 50-per cent, 70-per cent, 80-per cent, 90-per cent, and 100-per cent). The specimens were then passed through a series of various proportions of ethanol and Freon-TC (Freon-113) with a 20-minute period of immersion in each specified unit : a) three parts 100-per cent ethanol : one part Freon-TC, b) one part 100-per cent ethanol : one part Freon-TC, c) one part 100-per cent ethanol : three parts Freon-TC, and d) straight Freon-TC. A critical-point bomb, manufactured on the University of California Berkeley campus and similar to commercially-available models, was used to dry the samples from Freon-13 in approximately 20 minutes. The specimens were then attached to aluminum mounting stubs in horizontal position by means of conductive silver paint. A Varian ® vacuum evaporator (Model VE-10) was utilized to coat the samples with a metallic layer of platinum. The specimens were examined with a Coates and Welter ® scanning electron microscope (Model 50 Special), operating at an accelerating voltage of 15 to 16 kilovolts.

Results and Conclusions

Most observations were made in the lower ranges of magnification, approximately 30X to 200X, and a high voltage lens mode was utilized throughout the study. Magnifications greater than 100X

did not provide additional diagnostic benefit. Distortions of images were minimal with low-magnification SEM.

Electron scan of the cuticular surface of G. robustus revealed the following morphologic features. The body form is cylindrical for both males and females, decreasing in diameter toward the anterior and posterior ends. No areolae, pseudoareolae, or cuticular pores are present. The anterior extremity is essentially characterized by the same generalized appearance in both sexes (Figs. 20, 21). It is rounded in the shape of a hemisphere, and it may be separated from the body just behind by a very slight constriction. A rudimentary mouth, appearing as a slight depression, is discernible.

In female specimens of G. robustus, the posterior end is slightly enlarged in the shape of a bulb and obtusely truncated, with or without a slight vertical groove (Fig. 22). A cloacal opening, circular in appearance, is located terminal in the center of the truncated area.

The posterior extremity of the males has two lobes (Figs. 23-25). The caudal lobes are slightly-flattened on the inner side. On the ventral surface of the posterior end, anterior to the bifurcation, is a transverse postcloacal ridge which is crescent-shaped. The cloacal aperture, circular in outline, lies immediately anterior to the middle of the ridge.

No light-colored cuticular spots, pigmented neck-ring, or dark longitudinal bands, visible by LM, were discernible by SEM in the specimens examined. Apparently, the application of metallic coating (platinum) to the cuticular surface obscured such morphologic

features. Thus, while the technique of SEM may allow for clarification of some characters, it may mask others.

I believe SEM should not be considered a replacement for LM in the examination of hair-worms, but rather it should be used as an additional tool to gain further definition of morphologic and taxonomic features. Furthermore, I urge that investigators detail the procedure (individual steps) used in the preparation of gordian specimens for SEM study, as this may greatly affect the results.

SECTION 4

STUDIES ON THE IMMATURE (PREPARASITIC) STAGES OF Gordius robustus LEIDY.

I. Structure and Development

Introduction

Numerous reports have appeared in the scientific literature which appropriately describe the morphologic characters of mature specimens of Gordius robustus Leidy for purposes of diagnostic identification (Caballero y Caballero, 1936; Leidy, 1879; May, 1919; Montgomery, 1898a, 1898b; Thorne, 1940; and others). Histological studies have been published by May (1919) on the development of the parasitic stages of G. robustus in insect hosts. However, only scant information is available relating to the development and structure of the preparasitic stages of this gordian species. Both May (1919) and Thorne (1940) briefly discussed preparasitic larvae in the most general terms.

The present study was undertaken to further elucidate the developmental and structural characters of the preparasitic stages of G. robustus, including observations on oviposition, eclosion, and preparasitic larval development.

Materials and Methods

Active, free-living adult specimens (20 males and 25 females) of G. robustus, measuring 25 to 68 cm. in length and 0.5 to 1.8 mm. in greatest width, were collected by this author in fall-winter of 1974-75 from fresh-water sources in Contra Costa, Mendocino, Santa Clara, Solano, and Yolo Counties in Northern California (Figs. 26, 27). The worms were allowed to mate under laboratory conditions in vessels containing 68°F water at pH 6.5. Microscopic observations were made of spermatozoa, fertilized egg masses, and preparasitic larvae. No special stains or fixatives were used.

Results (Biological Studies) and Discussion

Fertilization. The mating behavior of G. robustus has been previously described by May (1919), who noted that the eggs were probably fertilized in the cloaca. In this study, fertilization was demonstrated to take place in the glandular antrum which is the anterior part of the female's cloaca. Although Thorne (1940) has suggested that fertilization may occur as eggs pass through the uterus, I observed no spermatozoa in the uterus of copulating females sacrificed within two hours after commencement of mating. However, numerous active spermatozoa, with a length of 5.5 to 13 μ, were seen in vibratory motion against the walls of egg masses recovered from the antral chamber of six female worms at the end of the same time period (Figs. 28, 29). Movement of the spermatozoa was very transient and ceased in approximately two to three minutes. No active movement was observed for spermatozoa collected from the lower cloaca or seminal receptacle. May (1919) considered that migration into

the seminal receptacle is probably passive and thereby could account for lack of movement of spermatozoa when placed on microscopic slide. I believe that environmental stresses from handling and changes in temperature, pressure, etc., may be detrimental to germ-cell vigor and could likewise influence the activity or motility of spermatozoa.

Oviposition. Female hair-worms deposited eggs over a period of one to two weeks, during which time the male worms were often seen wrapped around the females' bodies. Egg masses, consisting of thousands of individual eggs, were shed daily during the active period of egg laying, in strands of 1 to 2 cm. in length (Fig. 30). The initial color of the masses extruded from the female's gonopore was white but changed to tan over two to three weeks' time. Some females had degenerated anterior portions of the body, yet they continued to oviposit. Male gordiids* succumbed in one to three weeks after completion of mating, and females* died in two to four weeks after final oviposition. Aquatic fungi frequently contaminated vessels containing egg strings (Fig. 30), and the problem had to be combatted by frequent changing of the water in the containers and by the addition of minute amounts of fungicide (such as, 200-500 units Mycostatin® oral suspension** per gallon of water).

Embryology. The basic steps in the embryonic development of *G. robustus* were examined under microscope from the time of

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*The specimens were deposited in the collections of the author and the California Academy of Sciences, San Francisco, California.

*Manufactured by E. R. Squibb & Sons, Inc., Princeton, New Jersey.

fertilization (day 0) to the beginning of hatching (day 30) for egg strands kept in 68°F water at pH 6.5 (Table 1). Development on day 1 was characterized by groups of eggs with distinct outer membranes and granular material therein (Fig. 31). By day 2 the 2-cell stage and the beginning of second cleavage was observed; on days 3-4 the 4-cell and 8-cell stages were visible (Fig. 32). By days 5 and 6 the blastula stage was reached with the beginning of the formation of mesenchyme (Fig. 33). The formation of mesenchyme continued on days 6-8, and the beginning of gastrulation (invagination) was observed on day 8 (Fig. 34). The gastrula stage was completed by about day 10 or day 11, and the commencement of the formation of the proboscis was observed on day 11 (Fig. 35). By day 16 the larval outline was completed. On days 19 and 20, internal organs, such as the pseudointestine and glands, were somewhat differentiated (Fig. 36). Day 30 was the beginning date for eclosion with subsequent hatching on days 31, 32, and 33 (Fig. 37).

Eclosion. Eggs hatched in about 30 to 33 days in 68°F water kept at pH 6.5; eggs held in 50°F water at pH 6.5 hatched in 60 to 63 days; refrigerated eggs held in 39.2°F water at pH 6.5 failed to hatch (Table 2). Eggs held in either 50 or 39.2°F water at pH 6.5 for 15 days and then placed in 68°F water at pH 6.5 hatched in 40 to 45 days. When the pH of 68°F water was lowered slightly, from 6.5 to 6.0 or 5.5, the incubation period remained essentially the same--30 to 33 days. However, when the pH of 68°F water was raised, from 6.5 to 7 or 7.5, no hatching occurred. The pH of water at

sites of collection of mature gordiids ranged from 5.5 to 6.5. In one instance, I recovered a mass of egg strands from water with a pH of 6.0.

Larvae emerged from their eggshells via action of their proboscis which ruptured the protective membrane. Emergence took approximately five minutes once the eggshell was completely penetrated. Preparasitic larvae were observed to crawl slowly, by means of their proboscis and wriggling their postseptum from side to side (Fig. 37). Movement was increased when artificial lighting was intensified, and it slowed down to "normalcy" when brightness of illumination was reduced. Earlier, Thorne (1940) observed that the larvae of G. robustus lift themselves on the tips of their tails and swing about in circles, but this motion was not observed here.

Results (Morphological Descriptions) and Discussion

Eggs. Egg masses oviposited by the females measured 1 to 2 cm. in length and 1 to 1.5 mm. in width; each egg strand contained thousands of eggs. Individual eggs were 44 to 61 μ in diameter with shell thickness of 1.2 to 3.7 μ. Many eggs were observed to be enclosed by an extra outer membrane, appropriately 1 μ in thickness (Fig. 38). The outer membrane frequently united adjacent eggs in a link (Fig. 39).

Preparasitic Larvae. The preparasitic larvae of G. robustus in no way resemble their elongate parents (Figs. 40-46). The following description was prepared after examining hundreds of larvae by bright-field and phase-microscopy: total length, 106 to 150 μ;

length of preseptum 25 to 60 μ; length of postseptum 81 to 90 μ; presoma armed with 3 retractile stylets with retractor muscles and 3 circles of hooklets; the first circle of hooklets (nearest the stylets) is composed of 6 hooklets; the second circle of hooklets contains 6 larger hooklets; the outermost circle of pointed hooklets is composed of 6 scales which alternate between the hooklets of the other two circles; a paired hooklet of the outermost circlet gives the appearance of a seventh scale; the proboscis alternately extends outward to approximately 10 μ full length and then retracts backward; a gland duct extends from the lower end of the stylets to the base of the preseptum linking with the intestinal sac (or pseudointestine); the gland duct measures 0.15 to 0.25 μ in diameter along its length; globules and granules are small size, 1-5 μ in diameter, and appear scattered throughout the pseudointestine; a large gland, ovoid in shape and approximately 5 μ width by 15 μ length, often appeared in the lower portion of the pseudointestinal sac; an exit duct, 1 to 2 μ in diameter, leads from the lumen of the pseudointestine to the anal aperture; scattered mesenchymal cells are located posterior to the pseudointestine near the body wall and the adjacent duct; the posterior end of the body may be either pointed or blunt-shaped.

Over-all body length of the preparasitic larvae of G. robustus decreased to about two-thirds original length in a few days. Larvae lived 3-5 days in 68°F water at pH 5.5-6.5 and 5-6 days in 50°F water at pH 5.5-6.5. Dead, contracted larvae disintegrated within a few weeks. Neither larval encystment, as reported by

Dorier (1925, 1935) for Gordius aquaticus L., nor a quiescent state after hatching, as noted by Dorier (1933) for Gordionus violaceus (Baird), were observed in the present studies on G. robustus.

A comparison of the early development of various gordian species is summarized in Table 3. Females of G. robustus were observed to oviposit in the field in both the springtime (May, 1919) and fall/winter (present author). In contrast, oviposition in the field for other species was reported to have occurred in the spring (Inoue, 1958; Meissner, 1856; Müller, 1926).

SECTION 5

STUDIES ON THE IMMATURE (PREPARASITIC) STAGES OF *Gordius robustus* LEIDY.

II. Observations on the Effects of Drying

Introduction

Effects of drying upon the eggs and preparasitic larvae of the Gordioidea have been studied by previous investigators. In 1926, Müller reported that egg strands of *Gordius* with fully-differentiated larvae were removed from water for five days and when reimmersed still hatched. He concluded that perhaps drying of eggs was a condition for hatching. Rauther (1930) also considered that resistance to desiccation by gordian egg masses might be beneficial for the preparasitic larvae to be taken up by terrestrial insect hosts. However, Inoue (1960b) demonstrated that larvae of *Chordodes japonensis* Inoue hatch without drying and that drying proved unnecessary. He further observed that the larvae within their eggshells could not withstand drying for more than 24 hours.

According to Camerano (1892d), the preparasitic larvae of *Parachordodes pustulosus* (Baird) in the moist soil of cellars probably attack their coleopteran hosts, *Blaps*, directly. Such a

viewpoint appears to be based on the possible resisting power of the larval stage to desiccation. However, Inoue (1960b) found that the larvae of C. japonensis in moist soil cannot live longer and cannot preserve activity longer than in water. Furthermore, he observed that the preparasitic larvae of Chordodes do not creep into moist soil to protect themselves against desiccation.

In 1940, Thorne noted that exposure to air on a bamboo splinter for one minute was fatal to preparasitic larvae of Gordius robustus Leidy in every instance. Similarly, Inoue (1960b) demonstrated that drying for more than 20 seconds easily killed the larvae of C. japonensis.

The following studies were undertaken to reexamine more closely the effects of drying upon the eggs and preparasitic larvae of G. robustus and to report such findings.

Materials and Methods

Eggs containing fully-developed larvae and free preparasitic larvae of G. robustus, obtained from field-collected adults, were used. In experiment 1, egg strands were divided into various parts. Some were placed on microscopic slides, air-dried at approximately 68°F for 6, 12, 24, or 48 hours respectively, and then returned to 68°F water at pH 6.5, while others were constantly maintained in 68°F water at pH 6.5. The process of eclosion was subsequently studied to evaluate the influence of drying on development.

Experiment 2 was conducted to observe the activity of preparasitic larvae kept in moist soil; the technique of Inoue

(1960b) was followed with slight modifications. Two grams of dry soil were placed in a durable plastic dish (diameter, 25 mm.; depth, 4 mm.), and 1 cc. of water containing approximately 1,000 larvae was added on top the soil. After approximately 24-26 hours, larvae were examined for activity and compared with control larvae that had been kept in water.

The effects of drying upon survival of _G. robustus_ larvae were further studied in experiment 3. Groups of larvae were maintained and evaluated in a manner as described by Inoue (1960b). A drop of water containing preparasitic larvae was placed on a microscopic slide, and some water was removed by means of filter paper placed against the drop. At specific times (5, 10, 15, or 20 seconds) after the film of water on the surface of the larvae had been dried, a little water was added to them, and the larvae were examined for activity and structural changes (1, 1.5, 2, 2.5, 5, 15, 30, and >30 minutes later) and compared with control larvae kept in water.

Results and Conclusions

In experiment 1, it was observed that fully-developed larvae of _G. robustus_ do not need to be dried prior to hatching, contrary to the conclusions of Müller (1926) with _Gordius_ from the Old World. From Table 4, the results appear to indicate that dehydration is indeed detrimental to hatching, since many eggs were dried and failed to hatch. Inoue (1960b) observed that larvae of _Chordodes_, which hatched from desiccated egg strands, were generally contracted and

apparently inactive. Larvae of G. robustus hatched from desiccated egg strands in this experiment were similarly contracted and immobile.

From the results of experiment 2, it was shown that preparasitic larvae of G. robustus do not burrow into moist soil to protect themselves from drying. A moist-soil habitat may be undesirable compared to an aquatic habitat, since larvae remained on the surface of soil in a contracted, inactive state. On the other hand, larvae kept in water were active.

Experiment 3 indicated that G. robustus larvae are easily killed by desiccation when exposed for 20 seconds (Table 5). The larvae were contracted and showed no locomotion. However, most gordian larvae dried for 5-10 seconds revived when a little water was added to them. Preparasitic larvae that survived 5, 10, or 15 seconds of drying showed sluggish locomotion compared to control larvae kept in water.

The resisting power of the immature stages of G. robustus, the egg with developing larva therein and the subsequent free preparasitic larva, are quite sensitive to drying under the conditions noted in these experiments.

SECTION 6

EXPERIMENTAL AND NATURAL INFECTIONS OF *Gordius robustus* LEIDY IN VARIOUS HOSTS *

Introduction

There is still confusion surrounding the life cycle of the Gordioidea, particularly because of variations in development and maintenance of the immature preparasitic stages of the different species (Dorier, 1965). In brief, the life cycle of the gordian members of the Nematomorpha may be either direct or indirect. The preparasitic larvae of the hair-worms require a suitable host, such as an insect or other arthropod, to undergo developmental changes before the commonly-recognized, free-living adult stage is reached.

At least four possibilities exist as to the mode of infection by preparasitic gordian larvae: 1) the larvae appear on aquatic vegetation near the shoreline, in encysted-form, whereby they are subsequently eaten by suitable herbivorous insects and other hosts

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*Experimental animals utilized in these studies were maintained under laboratory conditions recommended by the Committee on the Revision of the Guide for Laboratory Animal Facilities and Care of the Institute of Laboratory Animal Resources, National Research Council, and by the Universities Federation for Animal Welfare.

and ultimately reach the mature state; 2) the larvae may actively penetrate the body wall of almost any soft-bodied aquatic or semi-aquatic organism, but perpetuation of the life cycle is maintained only when appropriately suitable hosts are parasitized; 3) the larvae, in either free- or encysted-form, are ingested from water by small aquatic or waterside animals wherein there occurs encystment or reencystment which represents a transitional step before final development is completed in larger carnivorous and omnivorous hosts; and 4) the larvae, in either encysted- or free-form, are consumed from water by large terrestrial insects and other arthropods in which they subsequently develop (Blunck, 1915, 1922, 1924; Camerano, 1888, 1892d, 1897a; Dorier, 1925, 1930, 1936, 1965; Houdemer, 1932; Inoue, 1960a, 1962a; Linstow, 1884, 1891b, 1898; Mahler, 1951; May, 1919; Meissner, 1856; Montgomery, 1899, 1904; Müller, 1920, 1926; Poinar and Doelman, 1974; Švábeník, 1925; Thorne, 1940; Villot, 1874, 1884a, 1891; and others).

The present investigation was undertaken to study the entry and development of immature forms of Gordius robustus Leidy in different animals and to elucidate the resultant pathologic findings. A field survey was also carried out to determine the various hosts of G. robustus in nature.

Materials and Methods

Mature specimens of G. robustus, 20 males and 25 females, were collected from Contra Costa, Mendocino, Santa Clara, Solano, and Yolo Counties in Northern California, and allowed to mate under

laboratory conditions in glass and plastic containers filled with distilled water at approximately 68°F and pH 5.5-6.5. Egg masses oviposited by the female gordiids were then allowed to develop into fully-differentiated larvae within their eggshells or subsequently into free preparasitic larvae.

Experimental infections were attempted in a number of ways: 1) by feeding fully-differentiated gordian larvae within their eggshells and newly-hatched preparasitic gordian larvae to mosquito larvae [*Aedes aegypti* (Linnaeus), *Aedes sierrensis* (Ludlow), *Culex pipiens* Linnaeus, and *Culex tarsalis* Coquillett], crickets [*Teleogryllus commodus* (Walker) and *Gryllus veletis* (Alexander and Bigelow)], grasshoppers [*Schistocerca nitens* (Thunberg)], wax moth larvae [*Galleria mellonella* (Linnaeus)], unidentified aquatic nymphs of Orders Ephemeroptera and Odonata, slugs (*Deroceras* spp.), snails (*Helix aspersa* Müller), goldfish [*Carassius auratus* (Linnaeus)], tadpole and adult Pacific tree frogs (*Hyla regilla* Baird and Girard), cockroaches [*Periplaneta americana* (Linnaeus) and *Leucophaea maderae* (Fabricius)], earthworms (*Eisenia* sp. and *Lumbricus terrestris* Linnaeus, California slender salamanders [*Batrachoseps attenuatus* (Eschscholtz)], sagebrush lizards (*Sceloporus graciosus* Baird and Girard), unidentified fresh-water leeches, laboratory mice (*Mus musculus* Linnaeus), and Syrian golden hamsters [*Mesocricetus auratus* (Waterhouse)]; 2) by injecting, via syringe and needle, fully-differentiated gordian larvae within their eggshells and newly-hatched preparasitic gordian larvae into the hemocoels of *S. nitens*, *P. americana*, and *G. veletis*; 3) by injecting, via syringe and needle,

fully-differentiated gordian larvae within their eggshells and newly-hatched preparasitic gordian larvae into the peritoneal cavities of H. regilla and M. musculus; 4) by inducing free preparasitic gordian larvae to penetrate the bodies of C. pipiens larvae and ephemerid naiads when placed side by side in a few drops of water; and 5) by feeding larvae of C. pipiens and C. tarsalis infected with gordian larvae to P. americana, S. nitens, and H. regilla.

Both vertebrate and invertebrate animals were collected at sites where adult specimens of G. robustus had been recovered. The animals were examined for parasitism by G. robustus or other hair-worms.

Results

Experimental attempts to infect various organisms by feeding G. robustus either as fully-differentiated larvae within their egg-shells or as newly-hatched preparasitic larvae were successful only with mosquito larvae. The other experimental animals failed to acquire infections by ingestion. Egg masses or preparasitic larvae of the hair-worm were readily ingested by second-, third-, and fourth-stage larvae of A. aegypti, A. sierrensis, C. pipiens, and C. tarsalis. The larvae of G. robustus could be observed in the hemocoel of the mosquito larvae within 20 minutes after exposure. Eggshells containing fully-differentiated gordian larvae were rapidly dissolved by the action of digestive juices in the alimentary tract. Preparasitic larvae passed into the midgut and vigorously penetrated the peritrophic membrane and adjacent epithelial cells of the intestine.

Next, the larvae moved into the hemocoel and frequently invaded musculature, hypodermis, and other tissues of dipteran hosts. Movement of the gordian larvae was accomplished by means of the proboscis, retractile stylets, and circlets of spines (Figs. 37, 45, 46). Oftentimes, the larval forms continued movement even after the onset of host reaction, that is, the deposition of melanin on the surface of the gordiids. Encasement of the gordian larvae in melanin started when the larvae entered the hemocoel, and it was complete by the time the parasites arrived at their final position in the host (Figs. 47, 48). Death of parasitic larvae took place as a result of the host defense reaction.

The penetration of 25 or more preparasitic gordian larvae into second-, third-, and fourth-stage mosquito larvae frequently resulted in the death of the hosts, possibly from massive trauma to the midgut, displacement of tissues, shock, or combinations thereof. The defense reaction which was characterized by excessive accumulation of melanin in heavily-parasitized hosts may have contributed in provoking pathologic change(s).

Attempts to induce infection by injecting G. robustus either as fully-differentiated larvae within their eggshells or as newly-hatched preparasitic larvae into the hemocoels of invertebrates or into the peritoneal cavities of vertebrates failed. Trials to infect larvae of C. pipiens and unidentified ephemerid naiads via penetration, when placed together with gordian larvae in a few drops of water, were unproductive.

The feeding of gordian larvae, via the infected larvae of C. pipiens and C. tarsalis, to cockroaches, grasshoppers, and adult tree frogs did not establish further infections. At dissection, the orthopterans and amphibians were observed to contain dead gordian larvae in their respective alimentary tracts.

Animals collected in the field, at sites where mature specimens of G. robustus had been recovered, were examined for the presence of gordian parasitism. The results are presented in Table 6. An aquatic damselfly nymph, collected in Contra Costa County, had 3 gordian larvae in the mid-gut (Fig. 49). The larvae were preparasitic, nonencysted forms. Identification of the gordian larvae was ascertained to be G. robustus, based on similarity in size and morphologic detail to preparasitic larval forms developed from egg masses that had been laid under laboratory conditions by adults of G. robustus obtained at the same site.

An adolescent female specimen of G. robustus, 40 cm. in length, was recovered from the hemocoel of an orthopteran, Stenopelmatus longispina Brunner, in Santa Clara County (Fig. 50). The hair-worm was active and survived in a container filled with water for approximately three hours. Its host, although alive when found in a puddle of water, was quite sluggish. A second hair-worm was collected from another Jerusalem cricket in the same area. However, both the parasite and its host were decomposed, and identity of the second gordiid could not be verified.

Discussion and Conclusions

Attempts to establish experimental infections of G. robustus in laboratory animals were successful only with mosquito larvae. Infections were established by feeding either egg masses containing fully-differentiated gordian larvae within their eggshells or free preparasitic forms to second-, third-, and fourth-stage mosquito larvae of four different species. These experimental findings, along with the recovery of preparasitic gordian larvae from a damselfly nymph which was collected in the field, indicate that G. robustus enters its host via the alimentary tract and not by penetration from the exterior. Furthermore, these observations agree with previous laboratory studies conducted by Inoue (1960a, 1962a) with Chordodes japonensis Inoue and Culex pipiens pallens Coquillett and by Poinar and Doelman (1974) with Neochordodes occidentalis (Montgomery) and Culex pipiens Linnaeus.

Poinar and Doelman (1974) observed that the larvae of N. occidentalis could be found in the hemocoels of C. pipiens larvae within 90 minutes after exposure. In the present studies, I observed larvae of G. robustus in the hemocoels of Aedes and Culex larvae just 20 minutes after placing gordiids and mosquitoes together in the same container of water.

Melanization of parasitic gordian larvae in insect hosts as noted in the present studies was similarly reported by Dorier (1930), Inoue (1962a), and Poinar and Doelman (1974) with other species of gordiids. The works of Salt (1963) and Poinar (1969, 1974) contain further discussions on melanization as a mechanism of insect immunity

to worms. I suggest that further studies, including ultrastructural investigations, be initiated to elucidate the complex mechanism(s) of insect immunity to gordian parasites.

Encystment of larval forms of G. robustus in hosts was not observed in the present studies. Similarly, neither May (1919) nor Thorne (1940) reported finding cysts of G. robustus in various arthropods which contained juvenile forms. However, Woodhead (1950) reported the presence of cystic forms of G. robustus in aquatic annelids (Cambarincola spp.).

The field survey for hosts of Gordius robustus and other hair-worms yielded few specimens that were parasitized. Conversely, May (1919), Thorne (1940), and others had collected large numbers of insect hosts infected with G. robustus.

The recovery of an adolescent specimen of G. robustus from a Jerusalem cricket found in a puddle of water emphasizes the host's attraction to water. Either the insect's desire to consume water in order to satisfy thirst or some kind of stimulus by the gordian parasite ready to emerge was involved (Edney, 1957; Hyman, 1951; Leclercq, 1946; Pennak, 1953). According to Cheng (1973), "The coincidence of the host's nearness to water and the emergence of young adults must be considered more than a matter of chance."

SECTION 7

GORDIAN WORMS AND WATER QUALITY RELATIONSHIPS, INCLUDING OBSERVATIONS ON TOLERANCE TO DISINFECTANTS

Introduction

The basic habitat of the Gordioidea is widely known and acknowledged to be a fresh-water environment. With the exception of the parasitic larval stage which undergoes metamorphosis and development in a variety of aquatic and terrestrial organisms, the life cycle of the gordian worm requires water. The fertilized egg masses, preparasitic larvae, and free-living adult forms exist in water of streams, ponds, rain puddles, and drinking troughs.

One plausible explanation for the numerous reported accounts of the recovery of gordian worms from the human alimentary tract is that the gordiids were consumed as free-living adults or as adolescent worms still within their insect hosts in drinking-water (Cowen and Williams, 1965; Faust *et al*., 1970). Likewise, the expulsion of hair-worms *per urethram* from a number of cases is attributed to infection of subjects during washing or bathing, and even douching with contaminated water ([illegible], [illegible]; [illegible] *et al*., 1968; Watson, 1960; and others).

There is occasional mention in the available literature concerning the presence of gordiids in potable water supplies or aquatic distribution systems. In 1870, Leidy reported that he saw on two occasions knotted masses of hair-worms which had passed through water pipes and issued at hydrants in the city of Philadelphia. Twenty-five years later, Reeker reported the presence of *Gordius* in an aqueduct in Neheim, West Germany. According to Whipple (1927), the hair-snake is one of many miscellaneous higher aquatic organisms found in American potable water supplies, but the author does not furnish details. A feasible but doubtful case of human gastrointestinal pseudoparasitism involving a hair-worm which may have passed through a public water supply was reported by Reardon (1928). In 1944, Baylis noted that the occurrence of gordian worms in domestic water supplies in England was documented at least 13 times; he further reported on two additional episodes wherein gordiids were recovered from water of a village pump and private well respectively. Pippet and Fernando (1961) cite the observation by the senior author of a gordian larva in tap water in Malaysia. In Salisbury, Rhodesia, Cowen and Williams (1965) reported the recovery of a gordiid, 13 cm. in length, from a household faucet while a consumer was filling her teakettle with tap water. Two unrelated episodes of potable water supply infestations by *Gordius* in Italy are documented by Foresi and Caroli (1968); in one instance, the authors noted that contamination of the drinking-water led to many cases of intestinal pseudoparasitism characterized by alimentary canal disturbances and malaise.

More recently, the present author recalls his own experience in 1968 of examining a viable male specimen of Gordius robustus Leidy, 50 cm. in length, which was recovered from water-carried sewage entering a municipal sewage treatment plant in a town in Northern California. The worm had apparently survived its journey through a sewer system collecting domestic and other wastes. It is possible, similar to the account mentioned previously by Reardon, that this gordiid may have actually moved through the town's drinking-water system and onto the discharge lines of the sewer system.

Since there is little information on the contemporary relationships of the Gordioidea to potable water supplies for either public or individual use, it is proper to evaluate some aspects of the subject. The specific objectives of this study were to: (1) ascertain the extent of the presence of gordian worms in American drinking-water supplies and distribution systems and (2) evaluate the tolerance of hair-worms against disinfection by various chemical agents.

Materials and Methods

Study 1. Survey of State and Territorial Health Jurisdictions. An extensive survey was conducted wherein the public health departments, or their counterparts, of the 50 states, territories, and possessions of this country were queried by mail and telephone; information was requested from the various health jurisdictions about the documentation of the recovery from or contamination of potable water supplies and distribution systems by members of the Gordioidea. Responses were accumulated and summarized.

Study 2. Tolerance of Gordian Worms Against Disinfection by Chemical Agents. Free-living adults and preparasitic larvae of the species *G. robustus* were used for the experiment. Thirty-five mature organisms were collected in Contra Costa, Mendocino, Santa Clara, Solano, and Yolo Counties in Northern California. Approximately 350 larvae were acquired from egg masses laid and incubated under laboratory conditions in distilled water of pH 6-6.5 and temperature 68°F.

Halazone N.N.R. (P-sulfonedichloramido-benzoic acid), commercially available from Abbott Laboratories, of North Chicago, Illinois, was supplied by the Water Quality Division, San Francisco City and County Water Department, Millbrae, California. The commercial product, which has widespread use as a water disinfectant, is packaged in tablet form; each tablet contains 0.004 gm. (1/16 grain) of Halazone with sodium borate and chloride.

Commercial sodium hypochlorite, or Chlorox® bleach, manufactured by Chlorox Company, Oakland, California, is available at a strength of approximately 5.25-per cent sodium hypochlorite or 2.5-per cent active chlorine. Household chlorine bleach of comparable strength is available under other trade names as well.

Crystalline iodine USP grade resublimed, was supplied by Dr. B. R. Visscher, University of California, Los Angeles campus, and Dr. F. H. Kahn, Beverly Hills, California.

Organisms were exposed to various concentrations of available chlorine or iodine in distilled water marketed by McGaw Laboratories, Division of American Hospital Supply Corporation, Glendale, California,

for a contact period of 30 minutes at average pH 6.5 and temperature 68°F: a) chlorine solution prepared from two Halazone tablets dissolved in one quart of water, b) chlorine solution prepared from four Halazone tablets dissolved in one quart of water, c) chlorine solution prepared from diluted, commercial sodium hypochlorite to an approximate strength of 1.5 mg./l., d) chlorine solution prepared from diluted, commercial sodium hypochlorite to an approximate strength of 5 mg./l., e) chlorine solution prepared from commercial sodium hypochlorite to an approximate strength of 20 mg./l., and f) iodine solution prepared from crystalline iodine by the method of Kahn and Visscher (1975). Iodine levels were computed rather than determined directly; whereas, initial and residual chlorine levels were carried out by the diethyl-p-phenylene diamine (DPD) method described in Taras *et al*. (1971).

Effects of disinfection upon gordian worms were determined in part by subjective observation, in that death was considered to have taken place if there was no movement of the adults after 30 minutes exposure to a given mode of treatment. Sluggish movement after treatment was considered to be a stunning effect upon the mature worms. No change in motility was taken to mean that chemical disinfection of water had no effect upon the adults. The inability of hair-worm larvae to penetrate through the intestinal cells and enter the body cavity of second- and third-stage *Culex pipiens* L. larvae after being ingested, was considered to indicate that disinfection of water by chemical means had an adverse effect upon the gordiids.

Due to the small numbers of specimens available for experimentation, the data only serve as examples of pilot trials on the kind of differences that may be expected in treated and control groups of worms (Hill, 1971).

Results and Discussions

Study 1. Survey of State and Territorial Health Jurisdictions. Responses to this author's query about the extent of the presence of hair-worms in potable water supplies and related systems of distribution were received from state epidemiologists or other public health specialists. Sixteen states noted that gordian worms had been reported in either water supplies or related distribution systems, while 34 states stated they had no records or documentation on the subject from their individual jurisdictions (see Table 7). No epidemiological data pertaining to gordiids were obtained from the various American territories and possessions.

It is apparent that the number of reported episodes of gordian worms in American domestic water supply systems or associated discharge lines (such as toilet bowls) are infrequent yet nevertheless of interest to the household consumer, water works operator, and public health specialist, since 16 states had record of such infestations. While some individuals may undoubtedly contend that such occurrences are unimportant, I feel that the presence of hair-worms in a potable water supply or related distribution system says something about water quality! Ingram and Bartsch (1960) appropriately noted that the presence of higher organisms in a system delivering water to the drinking vessels of consumers is an indication of defect.

Also, while it may be possible that some gordiids appear in toilet bowls, sinks, shower stalls, etc., as a result of emerging from the bodies of insects and other arthropods that have fallen into various plumbing fixtures, the bulk of the recovered specimens most likely have been transported through water-supply pipes. Baylis (1944) suspected that the presence of hair-worms in various domestic water supplies in the British Isles was attributed to parasitized insects passing into water distribution systems via unscreened cisterns or wells. Defects in a water-supply system in Italy were believed to have led to the entry of insects parasitized with Gordius which subsequently resulted in several cases of intestinal pseudoparasitism when soldiers drank water from the contaminated system (Foresi and Caroli, 1968). As noted by Mississippi health authorities, in the survey conducted by this author, the recovery of gordian worms from potable waters in that state coincides with periods of heavy cricket infestation and defects in the screening of a water-supply system. The storage of finished water supplies in uncovered distribution reservoirs or individual household water tanks may possibly contribute to the chances of waters becoming contaminated by organisms, including hair-worms (Cowen and Williams, 1965; Mackenthun, 1969; Phillips, 1968). Adequate screening and a complete covering over finished water supplies are advised for minimizing the presence of members of the Gordioidea in distribution systems or plumbing fixtures of consumers.

Study 2. Tolerance of Gordian Worms Against Disinfection by Chemical Agents. The results of exposing adults and larvae of

G. robustus to waters treated with various chemical disinfectants are summarized in Table 8. Halazone tablet effectiveness as a disinfectant depends mainly on combined residual chlorine whereas chlorine solution prepared from sodium hypochlorite depends largely on residual chlorine in the free form. Approximately 75 per cent of total available chlorine resulting from use of Halazone is in combined form while only about 10 per cent of total available chlorine resulting from use of diluted sodium hypochlorite is in such form. Residuals of chlorine resulting from use of two tablets of Halazone were ineffective in destroying adult gordiids within a 30-minute contact time, although such residuals partially destroyed the population of preparasitic larvae. The administration of four Halazone tablets to one quart of water proved sufficient to kill all larvae and most of the adults of *G. robustus*.

Disinfection of water with a low level of chlorine (1.8 ppm. initial and 1.2 ppm. residual) was shown to be insufficient to destroy either adults or preparasitic larvae. It should be noted at this point that a concentration of 0.5 to 1.0 ppm. or greater of residual chlorine for disinfection is routinely used in many American potable water systems (Brungs, 1973; Ehlers and Steel, 1965). Higher levels of chlorine (5.5 ppm. initial and 4.8 ppm. residual; 19.6 ppm. initial and 17.8 ppm. residual) prepared from sodium hypochlorite were more effective as disinfectants in destroying both adult and immature stages of *G. robustus*, but the resulting water is totally undrinkable. The disinfection of water by means of iodination (approximately 4 ppm.), prepared from crystalline iodine, proved

more effective than the disinfection powers of chlorine by either two tablets of Halazone or sodium hypochlorite solution at low level.

From a comparative standpoint, adult gordiids of Class Nematomorpha (Gordiacea) appear similar to mature nematodes in being quite resistant to levels of residual chlorine commonly used in many water systems (Anonymous, 1960; Bonetti and Tampieri, 1968; Chang, 1961; Chang _et al_., 1959; Chang _et al_., 1960a; Chang _et al_., 1960b; Engelbrecht and Austin, 1965; Kelly, 1955; Mackenthun, 1969; Merkley, 1970; Petit, 1975; Phillips, 1968; Román, 1972; Román and Rivas, 1971; Skeat and Dangerfield, 1969). In 1968, Foresi and Caroli reported that in two separate occasions superchlorination was utilized to rid potable water systems of contamination by hair-worms. Subsequent to massive chlorination, water quality of both Italian communities improved without further disturbances to environmental health. However, as Cooper (1974) appropriately noted ".... regardless of the degree of treatment, including disinfection and even sterilization, the complete removal of pathogenic organisms is a probability and not a certainty."

SECTION 8

HISTORICAL SKETCH OF GORDIAN HOST-PARASITE ASSOCIATIONS

A knowledge of the associations between members of the Gordioidea, the gordiids or hair-worms, and their various hosts dates from early times. However, confusion often developed regarding the specific identities of designated worm specimens, since early authors often used the same vernacular names for different worms, indicated no types, and gave imperfect descriptions. Thus, some measure of doubt and speculative assumption on the part of present-day investigators exists as to the exact identities implied. Up until the latter part of the nineteenth century, some investigators in the biomedical and biological sciences used the word "hair-worm" to refer to either the gordian worms, the mermithoid worms, or the filarial worms; others interpreted the term as being synonymous with either the Genus Mermis or Gordius; and still others used the word to mean specifically the Gordius (Girard, 1851; Hyman, 1951; Kirby and Spence, 1826; Riddell, 1928; Vejdovsky, 1886; and others). According to Villot (1874), medieval scholars clearly separated the hair-worms, or gordian worms, from forms which resembled them; the same author

further stated, "Avec Linné commence la confusion." On the other hand, Riddell (1928) has expressed the opinion that nematodes and gordiids were undoubtedly confused at times by writers in the Middle Ages. Girard (1851) and Montgomery (1899) reported that there were investigators, in the 1800's, who classified the gordian worms as annelids.

In Europe, during the Middle Ages, a belief arose that hair-worms originated from hairs of livestock, horses, etc., which had fallen into drinking troughs and there came to life (Hoeppli, 1959). Even in modern times, there are people who still believe that the gordiids spontaneously develop from animal-hairs in such fashion (Cappucci, 1973). A survey by this author among approximately 100 persons, who resided in the San Francisco Bay Area, revealed that at least 5 individuals accepted such a theory as being valid!

Another belief that apparently had its origin in medieval times was the concept that hair-worms were the progeny of serpents, and hence the vernacular usage of the term "hair-snake" during the Middle Ages (Faust _et al_., 1970; Riddell, 1928). According to Hausman (1923), this superstition was alluded to in Shakespeare's "Antony and Cleopatra," Act 1, Scene 2: "....Which like the courser's hair, hath yet but life, and not a serpent's poison." The supposed poisonous nature of these hair-snakes to man and beast was apparently believed by even some of the leading scholars of early Europe. In his classic writings of "De Natura Rerum," Thomas De Cantimpre (_circa_ 13th century a, b, and c) remarked on the poisonous consequences to man when hair-worms were consumed. Other early writers,

including Albertus Magnus (1519a and b) and Aldrovandus (1638a and b), mentioned similar grave consequences to man and beast upon ingestion of hair-worms. It is indeed most interesting from the standpoint of cultural anthropology and medical geography that Blanchard (1849) documented an account of similar belief among the Indian populations of Chile in the Western Hemisphere: "Se halla en las aguas dulcas de las cercaniás de Valparaiso, de Concepion y en otras provincias. Los indios lo temen mucho, y creen que si se introduce en su cuerpo les ocasiona graves enfermedades." In this century, Baylis (1944) reported the perpetuation of the belief among rural people of the British Isles, when he wrote the following passage, "The sender of a specimen from North Wales, for instance, quoted a local story that 'if a cow swallowed it she would be dead in a day or two.'" Baylis was referring to an adult gordiid sent to him for diagnostic examination.

In part, the more or less superstitious dread of hair-worms may have been due to confused and unclear diagnostic signs and symptoms associated with infections in man by the guinea worm, Dracunculus medinensis (Linnaeus). Erroneous misconceptions that hair-worms were capable of penetrating human skin or perforating through other tissues with resultant abscesses, ulcerations, etc., have persisted well into the 1800's in many parts of Europe (Anonymous, 1840; Bolschwing, 1842; Filipjev and Schuurmans Stekhoven, 1941; Hoeppli, 1959; Jordens, 1802; V[illegible], 1811). Unfortunately, similarity in the early classification of the guinea worms and gordiids may have complicated matters, since D. medinensis was

formerly designated *Gordius medinensis* L. and the true gordian worm was named *Gordius aquaticus* L. (Faust *et al*., 1970; Linnaeus, 1758; Schultz, 1970; Stiles and Hassall, 1920).

Together, the works of Krall (1959) and Riddell (1928) give a quick review of various gordian superstitions from the Old World which have been generated and preserved through the centuries. The present author was unable to retrieve citations pertaining to inclusions of hair-worms in the native folklore of North America, Africa, Australia, or the Far East. Works by North American authors are available which give reference to the superstitious tale among westerners of European descent that gordiids were the product of animal-hairs in standing waters. This latter belief was surely adopted from Old World influences (Girard, 1851; Leidy, 1853; Ward, 1918).

One of the earliest accounts of worms associated with insects is cited in the writings of Aldrovandus (1623). He reported that in the first century Pliny the elder took notice of the fact that worms appeared in the bodies of cockroaches. Both Aldrovandus and Lister (1672) respectively documented episodes wherein "hair-worms" (possibly gordiids?) were associated with insects. Years later, Rudolphi (1808-1810, 1819) published two classic works which included therein lists of vertebrate and invertebrate hosts known to be associated with worm parasites, including *Filaria*. Most likely, some of the parasites belonging to *Filaria* were gordiids. In 1828, Dufour published an article which is now considered one of the first undisputed accounts of an authentic host-parasite association involving a gordian worm.

Both Hope (1840) and Siebold (1842, 1843, 1848, 1850, 1854, 1856, 1858) prepared host lists and accompanying comments on a variety of insects that served as hosts for parasitic worms. The former author cited all worms under a single heading (Filaria) which probably included some gordiids. On the other hand, the latter worker used distinctive terminology to designate different worms, including the genera Gordius and Mermis.

In 1851, Diesing compiled an extensive list of parasitic associations involving protozoans, nematodes, and nematomorphs (gordiids) in a variety of hosts. The majority of citations pertaining to gordian worms as parasites dealt with insect-host species. Later, Diesing (1861) provided revisions to his earlier work.

The personal observations and travels of Asmuss (1858) resulted in the publication of a host list of various insect species parasitized by nematodes and gordiids. In his classic "Monographie des Dragonneaux," Villot (1874) included discussions and a list on gordian worms involved in host-parasite associations with insects. Linstow (1878, 1889) prepared two noteworthy lists of vertebrate and invertebrate animals serving as hosts for various worm parasites, including members of the Gordioidea. In 1885, Thompson published an extensive bibliography which included a number of citations on gordian worms as parasites. Subsequently, Camerano (1897a, 1915) compiled two comprehensive lists of vertebrate and invertebrate hosts associated with gordiids.

At the turn of the century, Schultz (1900) published a series of notes about parasitic worms in European Lepidoptera, including some references to gordian worms.

Since 1900, there have been other significant works and related references to gordian host-parasite associations, particularly with insects and other invertebrates. The index-catalogue prepared by Stiles and Hassall (1920) is perhaps one of the best resources for names of specific early authors and titles on various aspects of Class Gordiacea (Nematomorpha), including host-parasite associations with vertebrates and invertebrates. A rather thorough list of gordian worms in various hosts is presented in a paper published by Blunck (1922). Although Müller (1926) did not compile a host list, he published an article which discussed both earlier and original observations of associations between gordiids and their hosts. In 1928, Van Zwaluwenburg published a comprehensive host list of insects parasitized by Nematoda, Nematomorpha, and Acanthocephala. Two years later, Dorier (1930) presented his treatise on the biology and systematics of gordian worms. He included discussions on host-parasite relationships. Lists of insect hosts parasitized by members of the Gordioidea were included in the detailed works of Heinze (1937, 1941). In an attempt to update Van Zwaluwenburg's work on insect associations with nematodes, La Rivers (1949) published a review of the literature from 1926 to 1946. A total of eight insect genera or species were cited as hosts for gordian worms.

A list published by Jolivet and Théodoridès (1950) of various coleopterons known to have associations with helminths included one

citation of gordian parasitism in _Timarcha_ _tenebricosa_ (Fabricius).

In 1952, Inoue published an interesting article on the classification of Japanese _Chordodes_, and he included a list of associations between insect hosts and gordiids. Shortly after, Polozhentsev (1954) published a review of the literature on nematodes and nematomorphs in various insect hosts. The author furnished a bibliography of over 200 references from both Russian and western literature.

An extensive host list on the pathogens, parasites, and predators of medically important arthropods compiled by Jenkins (1964) included two citations on gordian parasites. More recently, Shephard (1974) reviewed the literature covering nematodes and nematomorphs as final hosts of arthropods, from 1900 through 1972, and he published an annotated bibliography which listed 45 gordian references.

Since the 1800's, a number of parasitic associations involving hair-worms and human beings have been documented (Faust _et_ _al_., 1970; Mattes and Wignand, 1958; Riddell, 1928; Stiles, 1907; Watson, 1960; and others). However, the authenticity of such associations have often been questioned (Cobbold, 1864; Faust _et_ _al_., 1975; Hegner _et_ _al_., 1938; and others). Nevertheless, many of the episodes are of some interest to medicine and public health because of the need for intervening health care or consultation. A review of the associations or cases of gordian worms in man is presented in another section of this dissertation.

It should also be noted that brief discussions on host-parasite associations between hair-worms and vertebrates other than man have been prepared by Flynn (1973), Reichenbach-Klinke (1962), and

Reichenbach-Klinke and Elkan (1965). The early literature on the role of non-human vertebrates as hosts for gordiids must be evaluated with care. For example, the documentation by Crisp (1873) of *Gordius* sp. in the lungs of sheep has been refuted by Cobbold (1873) to be merely an account of nematode parasitism.

Suggested Sources for Further Information

Excellent twentieth century reviews on general aspects of gordian biology, classification, and nomenclature have been published by Cheng (1973), Dorier (1965), Filipjev and Schuurmans Stekhoven (1941), Hyman (1951), Pennak (1953), and Rauther (1930). Brief, but very recent, commentaries on hair-worms have been authored by Dorier (1970), Hickman (1973), Inglis (1975), Kiryanova (1971), Rietschel (1974), and Storer *et al.* (1972).

SECTION 9

HOST LIST OF THE GORDIOIDEA : NEMATOMORPHA.

I. ANIMALS OTHER THAN MAN AS HOST

Introduction

General Considerations

While examining the literature on the host-parasite relationships of members of the Order Gordioidea, commonly called gordiids, gordian worms, or hair-worms, I became fascinated with the wide range of invertebrates and vertebrates that serve as their hosts. Generally speaking, gordiids have little host specificity (Dorier 1930, 1965; Pennak, 1953). The immature stages of hair-worms have been found in helminths, mollusks, annelids, arthropods, and chordates. Mature gordiids have been reported in fishes, amphibians, reptiles, birds, and mammals, including man.

The pathologic consequences to the various invertebrate and vertebrate hosts by the presence of hair-worms are not yet fully elucidated. However, a partial listing would include the following: 1) parasitic castration, reduction in bodyfat, tissue reaction and damage, and death in numerous cases involving insects and other arthropods (Balduf, 1939; Blunck, 1922; Camerano, 1897a; Dorier, 1930;

Filipjev and Schuurmans Stekhoven, 1941; Lipa, 1975; May, 1919; Meissner, 1856; Montgomery, 1904; Mrazek, 1926; Müller, 1926; Poinar and Doelman, 1974; Rees, 1973; Sahli, 1972; Steinhaus, 1967; Thorne, 1940; Weiser, 1966; Wülker, 1964; and others); 2) perforation of the alimentary tract with subsequent damage and displacement to visceral organs in a number of cases in fish (Nigrelli, 1941, 1943; Reichenbach-Klinke and Elkan (1965) and a case involving an amphibian (Clarke, 1831); and 3) numerous accounts of human cases characterized by either nervousness, colic, dysuria, or a number of other symptoms (Burger, 1972; Faust et al., 1970; Mattes and Wignand, 1958; Riddell, 1928; Rivas, 1920; Stiles, 1907; and others). Two human associations involved the surgical removal of gordiids from the external meatus and orbit respectively (Faust and Botero Ramos, 1960; Singh and Rao, 1966).

The economic significance of the gordian worms is related directly to the economic significance of the hosts (Filipjev and Schuurmans Stekhoven, 1941). For example, if the gordiids parasitize noxious hosts, such as grasshoppers, crickets, and other agricultural pests, then they would be considered beneficial, but if they destroy terrestrial Carabidae and preying mantids, which are beneficial, they would be considered economically undesirable. However, the relationships between gordiids and their various hosts warrant further detailed investigation; it may be that the hair-worms will someday commercially serve as useful biological control agents in insect population balance (Ki[illegible], 1954; Poinar and Doelman, 1974; and others). I recall from past readings in field crop production that

the federal government, in the 1800's, briefly investigated the possibility of using gordian worms to ward off impending attacks by locusts on American agriculture but abandoned the project in favor of other methods of control and because of limited monetary resources [reference unavailable].

A host list on the members of the Gordioidea was prepared, since the literature on the subject was widely scattered and often in little-known publications which were limited to the scientific community.

Orientation to the Host List

The following host list documents over 620 associations between gordian worms and animals other than man. Human associations with gordiids are covered in a separate section.

Strategic surveys of the literature were undertaken by both manual and computerized methods. Established informational pools, such as the Cataloging and Indexing System (CAIN) of the National Agriculture Library and the Medical Literature Analysis and Retrieval System on-Line (MEDLINE) were used. In addition, numerous personal contacts and communications with researchers, reference librarians, and other people interested in the project were utilized to provide references which might have been otherwise missed.

In preparing the host list, basic guidelines or standards had to be established. Both natural and experimental infections were documented in the available literature, although naturally occurring associations were originally favored. Consequently,

references referring to specific experimentally-created associations which probably occur in nature were also included in the host list. Attempts were made to exclude simple conjectures or associations later found to be erroneous.

The paradox arose as to the selection of specific references to cite for a given host-parasite association, particularly when two or more references were retrieved. The "most appropriate" reference may not always be the "most complete" one and vice versa, because of individual interpretations and opinions. Thus, I felt compelled in many instances to balance the selection of references by listing more than one author citation for a specific association.

To be included in the host list, at least the host genus and gordian family had to be known. But exceptions were made. For example, host unknowns were included if interesting biological observations had been reported on the associations. If possible, on the basis of the description provided, a name was supplied by the present author to a host or gordiid when no identification was furnished in the original reference.

Confusion and ambiguity frequently existed because of homonymy and synonymy in scientific names and differences in names of stated authorships and accompanying dates of original descriptions for specific species. For example, the same name, Gordius aquaticus, has been used by Linnaeus (1758) and Leidy (1846) to refer to specific gordiids. However, Leidy was indeed actually referring to a different species which he (1851a) later renamed G. varius and which Camerano (1897a) subsequently designated as Paragordius varius. The given

nomenclature of G. aquaticus, ascribed to Linnaeus, is recognized as being appropriate in designating the other distinct species (Hemming, 1958).

An effort was made to obtain the current, valid names of hosts and parasites. If confusion and disagreement still existed between a former and current scientific name, then both names were presented.

Geographic locations for host-parasite associations were not included in the list. Widespread ecologic studies are warranted to clarify the ranges of distribution of the various gordian worms, as a preliminary examination of the literature indicates that the distribution patterns of the hair-worms tend to overlap the ranges of distribution of the various host organisms and are not geographically restricted to a given locality.

The following references were used to elucidate the nomenclature of higher host categories: Blackwelder (1963), Blower (1974), Borror et al. (1976), Brinkhurst and Jamieson (1971), Cloudsley-Thompson (1968), Edmondson (1959), Grzimek (1972a-d, 1973a and b, 1974a-c, 1975a-d), Hickman (1973), Jordan (1963), Klemm (1972), Morton (1967), Pennak (1953), Pratt (1935), Rothschild (1961), Sawyer (1972), Sterba (1962), Storer et al. (1972), Walker et al. (1975), and Wheeler (1969).

Names of host families are listed in alphabetical order, with the various genera and species, in the left-hand column. Higher groups (such as, phyla and classes) are arranged according to the classification presented in Storer et al. (1972).

I followed Cheng (1973) and Dorier (1965, 1970) for the higher levels of gordian taxonomy (order and family categories), although other contemporary classifications were used, such as those of Inglis (1975), Kiryanova (1954), and Sciacchitano (1958).

Gordian nomenclature for a given host-parasite association is entered in the middle column of the list. Stage of gordian development is recorded under the scientific name. An abbreviated symbol before the scientific name of the hair-worm represents the family of that particular gordiid. These symbols and their corresponding gordian families are listed as follows: C-Chordodidae and G-Gordiidae.

Most beneficial to the preparation of the host list were the following publications on general zoological taxonomy: Blackwelder (1967), Mayr (1969), Ross (1974), Schenk and McMasters (1956), and Stoll *et al*. (1964). In addition, the following references on informational resources in the biological and biomedical sciences were extremely useful: Bottle and Wyatt (1971), Chamberlin (1952), Kerker and Murphy (1968, 1973), and Smith and Painter (1972).

HOST LIST. ANIMALS OTHER THAN MAN AS HOST

Phylum Platyhelminthes
Class Trematoda
Order Digenea
Family Brachycoeliidae

Brachycoelium hospitale (Stafford, 1900)	G-*Gordius* sp. (development stage)	Cort, 1915

Phylum Mollusca
Class Gastropoda
Order Stylommatophora
Family Helicidae

Arianta arbustorum (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930

Family Vitrinidae

Eucobresia diaphana (Draparnaud, 1805)	G-*Gordius* sp. (cystic stage)	Mahler, 1951
Vitrina pellucida (Müller, 1774)	G-*Gordius* sp. (cystic stage)	Mahler, 1951

Order Basommatophora
Family Ancylidae

Ancylus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930

Family Lymnaeidae

Lymnaea sp.	G-*Gordius* sp. (cystic stage)	Jeffreys, 1833
Lymnaea pereger (Müller, 1774)	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Dorier, 1930
Lymnaea pereger (Müller, 1774)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Chitwood and Chitwood, 1937; Dorier, 1930

Lymnaea pereger (Müller, 1774)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Camerano, 1897a; Dorier, 1930
Lymnaea pereger (Müller, 1774)	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Camerano, 1915; Chitwood and Chitwood, 1937
	Family Physidae	
Physa fontinalis (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930
	Family Planorbidae	
Planorbis sp.	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Dorier, 1930
Planorbis sp.	G-*Gordius* sp. (cystic stage)	Linstow, 1883a, 1889; Villot, 1874
Planorbis sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930; Rolleston, 1888
Planorbis sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Blunck, 1922; Dorier, 1930
Planorbis sp.	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Dorier, 1930
Planorbis carinatus Müller, 1774	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1925, 1926
	Unstated family	
Unstated spp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Dorier, 1930

	Phylum Annelida Class Oligochaeta Order Plesiopora Family Enchytraeidae	
Enchytraeus albidus Henle, 1837	G-*Gordius* sp. (cystic stage)	Camerano, 1915; Linstow, 1878
Enchytraeus vermicularis Hoffmeister, 1843	G-*Gordius* sp. (cystic stage)	Linstow, 1883a, 1889; Villot, 1874
Fridericia sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Blunck, 1922; Müller, 1920
	Family Naididae	
Nais sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Dorier, 1930; Meissner, 1856
	Family Tubificidae	
Tubifex sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930
	Order Prosopora Family Branchiobdellidae	
Cambarincola spp.	G-*Gordius robustus* Leidy, 1851 (cystic stage)	Woodhead, 1950
Cambarincola spp.	C-*Paragordius varius* (Leidy, 1851) (cystic stage)	Woodhead, 1941, 1950
	Order Opisthopora Family Lumbriculidae	
Lumbriculus limosus Leidy, 1850	C-*Paragordius varius* (Leidy, 1851) (cystic stage)	Leidy, 1858

Class Hirudinea
Order Rhynchobdellida
Family Glossiphoniidae

Glossiphonia spp. [=*Clepsine* spp.]	G-*Gordius tenuis* Leidy, 1878 (developmental stage)	Leidy, 1878

Order Pharyngobdellida
Family Erpobdellidae

Erpobdella octoculata (Linnaeus, 1758)	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Dorier, 1930
Erpobdella octoculata (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Villot, 1874, 1891
Erpobdella octoculata (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Dorier, 1930
Erpobdella octoculata (Linnaeus, 1758)	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Blunck, 1922; Dorier, 1930
Erpobdella punctata (Leidy, 1870)	G-*Gordius* sp. (developmental stage)	Sawyer, 1971
Mooreobdella microstoma (Moore, 1901) [=*Dina* (*Mooreobdella*) *microstoma*]	G-*Gordius* sp. (developmental stage)	Sawyer, 1971

Phylum Arthropoda
Subphylum Chelicerata
Class Arachnida
Order Scorpionida
Family Vaejovidae [=Vejovidae]

Uroctonus mordax Thorell, 1876	Unstated sp. Gordioidea (development stage)	Toren, 1975

Order Araneae [=Araneida]
Family Araneidae

Aranea ceropegia Walckenaer, 1802	G-*Gordius epeirae-ceropegiae* Diesing, 1851 (developmental stage)	Diesing, 1851
Aranea diadema Linnaeus, 1758	G- ? *Gordius epeirae-diademae* Diesing, 1851 (developmental stage)	Diesing, 1851

Family Ctenidae

Ctenus byrrhus (Simon, 1888) [?=*Ctenus bryrrbus* as cited by Acholonu, 1968]	C-*Neochordodes* sp. (developmental stage)	Acholonu, 1968

Family Gnaphosidae

Gnaphosa lucifuga (Walckenaer, 1802) [=*Drassus fuscus* Latreille, 1806]	G-*Gordius drassi-fusci* Diesing, 1851 [?=*Gordius aquaticus* Linnaeus, 1758] (developmental stage)	Blunck, 1922; Diesing, 1851 Siebold, 1848
Gnaphosa lucifuga (Walckenaer, 1802)	G-*Gordius drassi-lucifugi* Diesing, 1851 (developmental stage)	Diesing, 1851
Gnaphosa lucifuga (Walckenaer, 1802)	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Camerano, 1915; Siebold, 1856

Family Phalangiidae

Phalangium cornutum Linnaeus, 1767	G-*Gordius truncatulus* (Rudolphi, 1809) (developmental stage)	Diesing, 1851
Phalangium opilio Linnaeus, 1758	G-*Gordius truncatulus* (Rudolphi, 1809) (developmental stage)	Diesing, 1851

Family Phrynidae

Phriniscus bacillifer Gerstäcker, 1873 [=Phryniscus bacillifer]	C-Beatogordius sankurensis Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958

Unstated family(ies)

Unstated sp.	G-Gordius sp. (developmental stage)	Clementi, 1869
Unstated sp.	G-Gordius aquaticus (developmental stage)	Camerano, 1915; Römer, 1895b
Unstated sp. [?=Aranea sp.]	G-Gordius araneae (Rudolphi, 1809) [?=Gordius aquaticus Linnaeus, 1758] (developmental stage)	Diesing, 1851

Subphylum Mandibulata
[or Antennata]
Class Crustacea
Subclass Branchiopoda
Order Notostraca
Family Apodidae

Triops (Apus) cancriformis (Bosc, 1801)	G-Gordius api-cancriformis Diesing, 1851 [=Gordius apodis-cancriformis] (developmental stage)	Diesing, 1851; Linstow, 1878

Subclass Copepoda
Order Podoplea [=Cyclopoida]
Family Cyclopidae

Cyclops sp.	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Blunck, 1922; Meissner, 1856

Subclass Malacostraca
Order Isopoda
Family Oniscidae

Oniscus sp.	C-*Paragordius varius* (Leidy, 1851) (cystic stage)	Montgomery, 1904

Order Amphipoda
Family Gammaridae

Gammarus sp.	C-*Paragordius varius* (Leidy, 1851) (cystic stage)	Montgomery, 1904

Order Podophthalmia [or Decapoda]
Family Caridae [or Atyidae]

? *Caridina* sp.	G-*Gordius* sp. (developmental stage)	Linstow, 1878

Class Insecta
Subclass Apterygota
Order Thysanura
Family Campodeidae

Campodea (Paurocampa) pretneri Condé, 1974	? G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Bareth, 1974
Plusiocampa bulgarica Silvestri, 1931	? G-*Gordius aquaticus* Linnaeus, 1758 (cystic and developmental stages)	Bareth, 1974
Plusiocampa bulgarica Silvestri, 1931	? C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic and developmental stages)	Bareth, 1974
Plusiocampa pucketti Conde in Bareth, 1974	? C-*Paragordius tricuspidatus* (Dufour, 1828) [? =*Paragordius varius* (Leidy, 1851)] (cystic stage)	Bareth, 1974

Subclass Pterygota
Order Odonata
Family Corduliidae

Somatochlora metallica (Van der Linden, 1825)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858

Family Libellulidae

Orthetrum cancellatum (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Assmuss, 1858
Sympetrum flaveolum (Linnaeus, 1758)	G-*Gordius libellulae-flaveolae* Diesing, 1851 (developmental stage)	Diesing, 1851
Sympetrum pedemontanum (Allioni, 1766)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858
Sympetrum vulgatum (Linnaeus, 1758) [=*Sympetrum variegata* (Müller, 1764)]	G-*Gordius libellulae-variegatae* Diesing, 1851 (developmental stage)	Diesing, 1851
Unstated sp.	C-*Euchordodes libellulovivens* Heinze, 1937 (developmental stage)	Heinze, 1937

Undetermined family

Undetermined sp.	G-*Gordius robustus* Leidy, 1851 (preparasitic larval form, in alimentary tract)	Present author, in this dissertation

Order Ephemeroptera [=Ephemerida]
Family Baetidae

Baetis spp.	C-*Paragordius* sp. (developmental stage)	White, 1969
Baetis sp.	C-*Paragordius varius* Leidy, 1851 (developmental stage)	White, 1966

Cloeon dipterum (Linnaeus, 1761)	C-*Chordodes japonensis* Inoue, 1952 (cystic stage)	Inoue, 1960a, 1962a
Cloeon dipterum (Linnaeus, 1761)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930
Cloeon dipterum (Linnaeus, 1761)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Linstow, 1889; 1892
	Family Ephemerellidae	
Ephemerella spp.	C-*Paragordius* sp. (developmental stage)	White, 1969
	Family Ephemeridae	
Ephemera vulgata Linnaeus, 1758	G-*Gordius aquaticus* (Linnaeus, 1758) (cystic stage)	Linstow, 1883a; Meissner, 1856
Ephemera vulgata Linnaeus, 1758	C-*Parachordodes tolosanus* (Dujardin, 1842) (?cystic and developmental stages)	Linstow, 1889 1891b; Meissner, 1856
	Family Heptageniidae	
Epeorus torrentium Eaton, 1881	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Dorier, 1925, 1926
	Family Leptophlebiidae	
Leptophlebia sp.	C-*Paragordius* sp. (developmental stage)	White, 1969
	Unstated family	
Unstated sp.	G-*Gordius* sp. (developmental stage)	Mellanby, 1951
	Order Orthoptera Family Acrididae	
Arcyptera fusca (Pallas, 1773)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858

Calliptamus italicus (Linnaeus, 1758)	G-Gordius calliptami-italici Diesing, 1851 (developmental stage)	Diesing, 1851
Caloptenus spretus Walsh, 1866	G-Gordius robustus Leidy, 1851 (developmental stage)	Riley et al., 1878
Chorthippus biguttulus (Linnaeus, 1758)	G-Gordius oedypodae-biguttulae Diesing, 1851 (developmental stage)	Diesing, 1851
Chorthippus parallelus (Zetterstedt, 1821)	G-Gordius oedypodae-parallelae Diesing, 1851 (developmental stage)	Diesing, 1851
Diedronotus discoideus (Serville, 1831)	G-Gordius acrydii Diesing, 1851 (developmental stage)	Diesing, 1851
Locusta sp.	G-Gordius sp. [or possibly a filarial nematode] (developmental stage)	Siebold, 1854
Locusta sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Linstow, 1898; Mrazek, 1926
Locusta sp.	G-Gordius locustarum Oken, 1815 (developmental stage)	Oken, 1815; Stiles and Hassall, 1920; Van Zwaluwenburg, 1928
Locusta hemitogia (auct.?) (nomen nudum)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Diesing, 1851; Linstow, 1898; Siebold, 1842
Locusta migratoria Linnaeus, 1758 [=Locusta danica Linnaeus, 1767]	G-Gordius oedypodae-migratoriae Diesing, 1851 (developmental stage)	Diesing, 1851; Siebold, 1842, 1843, 1850
Locusta migratoria cinerascens (Fabricius, 1781)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1925, 1926

Locusta migratoria migratoroides (Reiche and Fairmaire, 1847?)	G-Gordius sp. (developmental stage)	Mackie, 1913; Van Zwaluwenburg, 1928
Locustina sp. [Some taxonomists classify this species as being in Family Tettigoniidae.]	G-Gordius locustinae Diesing, 1851 [?=Gordius locustarum Oken, 1815] (developmental stage)	Diesing, 1851; Stiles and Hassall, 1920
Melanoplus bivittatus (Say, 1825)	G-Gordius robustus Leidy, 1851 (developmental stage)	Riley et al., 1878
Melanoplus femur-rubrum (DeGeer, 1773)	G-Gordius sp. [or possibly Mermis sp.] (developmental stage)	Cosens, 1915
Melanoplus spretus (Thomas, 1865)	G-Gordius robustus Leidy, 1851 (developmental stage)	Riley, 1875, cited in Rees, 1973
Oedipoda caerulescens (Linnaeus, 1758)	G-Gordius oedypodae-coerulescentis Diesing, 1851 (developmental stage)	Diesing, 1851; Siebold, 1848
Omocestus viridulus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Siebold, 1856
Oxya chinensis (Thunberg, 1815)	G-Gordius sp. (developmental stage)	Van Zwaluwenburg, 1928
Schistocerca americana paranensis (Burmeister, 1861)	G-Gordius acridiorum Weyenbergh, 1879 (developmental stage)	Camerano, 1897a; Linstow, 1889
Stauroderus sp.	G-Gordius sp. (developmental stage)	Codina, 1925; Van Zwaluwenburg, 1928
Stenobothrus sp.	G-Gordius sp. (developmental stage)	André, 1927; Dorier, 1930
Truxalis sp.	G-Gordius sp. (developmental stage)	Dorier, 1930; Villot, 1874

Unstated spp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Diesing, 1851; Römer, 1895b; Siebold, 1842
Unstated spp.	G-*Gordius robustus* Leidy, 1851 (developmental stage)	Montgomery, 1907; Ward, 1918
Unstated sp.	C-*Neochordodes occidentalis* (Montgomery, 1898) (developmental stage)	Montgomery, 1907; Ward, 1918
	Family Blaberidae [Some authors put in Order Dictyoptera.]	
Blaberus giganteus (Linnaeus, 1758) [=*Blabera gigantea*]	C-*Chordodes pilosus* Möbius, 1855 (developmental stage)	Janda, 1894; Möbius, 1855
	Family Blattellidae [Some authors put in Order Dictyoptera.]	
Margattea beauvoisi (Walker, 1868)	C-*Beatogordius raphaelis* (Camerano, 1893) (developmental stage)	Camerano, 1893, 1897a, 1915
Symploce parenthesis (Gerstäcker, 1883)	C-*Beatogordius raphaelis* (Camerano, 1893) (developmental stage)	Camerano, 1893, 1897a, 1915
	Family Blattidae [Some authors put in Order Dictyoptera.]	
Blatta sp.	C-*Beatogordius raphaelis* (Camerano, 1893) (developmental stage)	Sciacchitano, 1958
Blatta sp.	C-*Chordodes capensis* Camerano, 1895 (developmental stage)	Sciacchitano, 1958
Blatta sp.	C-*Chordodiolus echinatus* (Linstow, 1901) (developmental stage)	Sciacchitano, 1958

Blatta sp.	G-? Gordius aquaticus Linnaeus, 1758 [?=Gordius robustus Leidy, 1851] or [?=Paragordius varius (Leidy, 1851)] (developmental stage)	Stiles and Hassall, 1894
Blatta orientalis Linnaeus, 1758	G-Gordius blattae-orientalis Diesing, 1851 (developmental stage)	Diesing, 1851
Blatta orientalis Linnaeus, 1758	C-Neochordodes moraisi Carvalho, 1942 (developmental stage)	Carvalho, 1942
Blatta orientalis Linnaeus, 1758	C-Paragordius varius (Leidy, 1851) (developmental stage)	Leidy, 1878
Periplaneta sp.	C-Chordodes iturensis Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
?Periplaneta americana (Linnaeus, 1758) or ?Blatta orientalis Linnaeus, 1758	G-Gordius orientalis Dolley, 1894 (developmental stage)	Dolley, 1894, cited in Stiles and Hassall, 1920
Unstated sp.	C-Chordodes morgani Montgomery, 1898 (developmental stage)	Montgomery, 1907; Ward, 1918
Unstated sp.	C-Chordodes puerilis Montgomery, 1898 (developmental stage)	Montgomery, 1898a
	Family Gryllacrididae [=Gryllacridae]	
Diestrammena japonica Karny, 1930 [?=Diestrammena japonica Blatchley, 1920]	G-Gordius sp. (developmental stage)	Inoue, 1975
Stenopelmatus fuscus Haldeman, 1852 [=Stenopelmatus fasciatus Thomas, 1872]	G-Gordius robustus Leidy, 1851 (developmental stage)	Riley et al., 1878; Thorne, 1940

Stenopelmatus fuscus Haldeman, 1852 [=Stenopelmatus fasciatus Thomas, 1872]	Unstated spp. Gordioidea (developmental stage)	Helfer, 1963
Stenopelmatus longispina Brunner, 1888	G-Gordius robustus Leidy, 1851 (developmental stage)	Present author, in this dissertation
	Family Gryllidae	
Acheta sp. [?=Gryllus sp.]	C-Paragordius varius (Leidy, 1851 (developmental stage)	Montgomery, 1907
Acheta domesticus (Linnaeus, 1758)	G-Gordius sp. (developmental stage)	Linstow, 1878, 1889; McCook, 1884
Gryllomorpha dalmatina (Ocskay von Ocksö, 1832)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Corbel, 1967
Gryllus sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Dorier, 1930; Mrazek, 1926
Gryllus sp.	G-Gordius grylli Diesing, 1851 (developmental stage)	Diesing, 1851
Gryllus sp.	G-Gordius locustarum Oken, 1815 [?=Gordius locustinae Diesing, 1851]	Oken, 1815; Stiles and Hassall, 1920
Gryllus sp. [=Liogryllus sp.]	Unstated sp. Gordioidea (developmental stage)	Filipjev and Schuurmans Stekhoven, 1941
Gryllus assimilis (Fabricius, 1775)	C-Paragordius varius (Leidy, 1851) (developmental stage)	Ackert and Wadley, 1921; May, 1919; Tanner, 1939
Gryllus campestris Linnaeus, 1758 [=Acheta campestris]	G-Gordius grylli-campestris Diesing, 1851 (developmental stage)	Diesing, 1851; Linstow, 1878; Siebold, 1850

Gryllus neglectus Scudder, 1862	G-Gordius robustus Leidy, 1851 (developmental stage)	Riley et al., 1878
Gryllus pennsylvanicus Burmeister, 1838	G-Gordius sp. (developmental stage)	Girard, 1851; Siebold, 1854
Gryllus pennsylvanicus Burmeister, 1838	C-Paragordius varius (Leidy, 1851) (developmental stage)	Montgomery, 1903
Pteronemobius fasciatus (DeGeer, 1773)	C-Paragordius varius (Leidy, 1851) (developmental stage)	May, 1919
Tartarogryllus burdigalensis (Latreille, 1804)	C-Paragordius stylosus (Linstow, 1883) (developmental stage)	Heinze, 1937, 1941
Tartarogryllus burdigalensis (Latreille, 1804)	C-Paragordius tricuspidatus (Dufour, 1828) [=Gordius grylli-bordigalensis Diesing, 1851] [=Gordius dectici-albifrontis Diesing, 1851] (developmental stage)	Blunck, 1922; Dufour, 1828; Linstow, 1878
	Family Mantidae [Some authors put in Order Dictyoptera.]	
Deroplatys sp.	C-Chordodes furnessi Montgomery, 1898 (developmental stage)	Montgomery, 1898c
Hierodula sp.	C-Chordodes furnessi Montgomery, 1898 (developmental stage)	Montgomery, 1898c
Hierodula basalis (Haan, 1842)	C-Chordodes baramensis (Römer, 1895) (developmental stage)	Römer, 1895a, 1896
Hierodula dyaka Westwood, 1889	C-Chordodes shipleyi Camerano, 1899 (developmental stage)	Shelford, 1902

Hierodula gastrica (Stål, 1858)	C-Chordodes ferox Camerano, 1897 [=Gordius verrucosus Baird, 1853] (developmental stage)	Sciacchitano, 1958
Hierodula membranacea (Burmeister, 1838)	C-Chordodes ferox Camerano, 1897 [=Gordius verrucosus Baird, 1853] (developmental stage)	Bell, 1885; Camerano, 1897a
Hierodula transcaucasia Brunner, 1878	C-Chordodes longipilus Kiryanova, 1949 (developmental stage)	Bogush, 1971; Kiryanova, 1971
Hierodula viridis (Forskål, 1775)	C-Chordodes ferox Camerano, 1897 [=Gordius verrcosus Baird, 1853] (developmental stage)	Bell, 1885; Camerano, 1897a
Idoleum diabolicum (Saussure, 1869-70) [=Idolum diabolicum]	C-Chordodes ferox Camerano, 1897 [=Gordius verrucosus Baird, 1853] (developmental stage)	Bell, 1885; Camerano, 1897a
Idolomorpha defoliata (Serville, 1839)	G-Gordius granulosus Linstow, 1897 (developmental stage)	Camerano, 1915; Linstow, 1897
Mantis sp.	C-Chordodes ambionensis Sciacchitano, 1963 (developmental stage)	Sciacchitano, 1963
Mantis sp.	C-Chordodes caledoniensis (Villot, 1874) [=Gordius tuberculatus Villot, 1874] (developmental stage)	Camerano, 1897a; Villot, 1874
Mantis sp.	C-Chordodes congolensis Sciacchitano, 1933 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes ferox Camerano, 1897 [=Gordius verrucosus Baird, 1853] (developmental stage)	Camerano, 1897a

Mantis sp.	C-Chordodes hawkeri Camerano, 1892 (developmental stage)	Camerano, 1915
Mantis sp.	C-Chordodes kivuensis Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes kolensis Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes ligasiensis Sciacchitano, 1933 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes maculatus Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes madagascariensis (Camerano, 1893) (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes mobensis Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
Mantis sp.	C-Chordodes montgomeryi Camerano, 1901 (developmental stage)	Camerano, 1915
Mantis sp.	C-Chordodes moutoni Camerano, 1895 [=Chordodes montoni] (developmental stage)	Camerano, 1915; Shipley, 1903
Mantis sp.	C-Chordodes ornatus (Grenacher, 1868) (developmental stage)	Linstow, 1878; Villot, 1874
Mantis sp.	C-Chordodes oscillatus Kiryanova, 1953 (developmental stage)	Kiryanova, 1953
Mantis sp.	C-Chordodes shipleyi Camerano, [illegible] (developmental stage)	Camerano, 1899; 1915

<u>Mantis</u> sp.	C-<u>Chordodes</u> <u>siamensis</u> Camerano, 1903 (developmental stage)	Camerano, 1915
<u>Mantis</u> sp.	C-<u>Chordodes</u> <u>skorikowi</u> Camerano, 1903 (developmental stage)	Camerano, 1915
<u>Mantis</u> sp.	C-<u>Chordodes</u> <u>undulatus</u> Linstow, 1906 (developmental stage)	Linstow, 1906b
<u>Mantis</u> sp.	G-<u>Gordius</u> sp. (developmental stage)	Green, 1902; Houdemer, 1938; Laboulbène, 1864; Lataste, 1896, in Camerano, 1897a; Linstow, 1878
<u>Mantis</u> sp.	G-<u>Gordius</u> <u>aquaticus</u> Linnaeus, 1758 (developmental stage)	Mrazek, 1926; Rolleston, 1888
<u>Mantis</u> sp.	C-<u>Neochordodes</u> <u>annandalei</u> (Camerano, 1908) (developmental stage)	Camerano, 1915
<u>Mantis</u> <u>religiosa</u> (Linnaeus, 1758) [Some taxonomists do not place parentheses about the author's name.]	C-<u>Chordodes</u> <u>ibembensis</u> Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
<u>Mantis</u> <u>religiosa</u> (Linnaeus, 1758)	C-<u>Chordodes</u> <u>maculatus</u> Sciacchitano, 1958 (developmental stage)	Sciacchitano, 1958
<u>Mantis</u> <u>religiosa</u> (Linnaeus, 1758)	C-<u>Chordodes</u> <u>madagascari-ensis</u> (Camerano, 1893) (developmental stage)	Sciacchitano, 1958
<u>Mantis</u> <u>religiosa</u> (Linnaeus, 1758)	G-<u>Gordius</u> <u>aquaticus</u> Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Gliesch, 1933; Linstow, 1889

Polyspilota aeruginosa pustulata (Stoll, 1813)	G-Gordius mantidis-pustulatae Linstow, 1879 (developmental stage)	Linstow, 1889
Popa undata (Fabricius, 1793)	C-Chordodes hawkeri Camerano, 1902 (developmental stage)	Camerano, 1915
Rhombodera scutata Karsch, 1892 [?=Hierodula scutata Bolivar, 1889]	C-Chordodes capillatus Linstow, 1901 (developmental stage)	Camerano, 1915; Linstow, 1901
Rhombodera valida (Burmeister, 1838) [=Hierodula valida]	C-Chordodes baramensis Römer, 1895 (developmental stage)	Römer, 1895c, cited in Van Zwaluwenburg, 1928
Rhombodera valida (Burmeister, 1838) [=Hierodula valida] [=Rhombodera basalis Stål, 1877]	C-Chordodes shipleyi Camerano, 1899 (developmental stage)	Shelford, 1903
Sphodromantis scutata (auct.?) (nomen nudum?) [?=Hierodula scutata Bolivar, 1889] or [?=Rhombodera scutata Karsch, 1892]	C-Chordodes madagascariensis (Camerano, 1893) (developmental stage)	Inoue, 1952
Stagmatoptera spp. [other than S. precaria (Linnaeus, 1758)]	C-Chordodes brasiliensis Janda, 1894 (developmental stage)	Carvalho, 1946b
Stagmatoptera hyaloptera (Perty, 1832)	C-Chordodes brasiliensis Janda, 1893 (developmental stage)	Camerano, 1897b
Stagmatoptera precaria (Linnaeus, 1758)	C-Chordodes brasiliensis Janda, 1893 (developmental stage)	Carvalho, 1946a and b
Stagmatoptera precaria (Linnaeus, 1758)	G-Gordius tenuis Weyenbergh, 1879 (developmental stage)	Camerano, 1897a; Linstow, 1889

Tenodera angustipennis Saussure, 1869	C-Chordodes fukuii Inoue, 1951 (developmental stage)	Inoue, 1952
Tenodera angustipennis Saussure, 1869	C-Chordodes japonensis Inoue, 1952 (developmental stage)	Inoue, 1952
Tenodera aridifolia (Stoll, 1813)	C-Chordodes tenoderae Kiryanova, 1957 (developmental stage)	Kiryanova, 1957
Tenodera sinensis Saussure, 1871	C-Chordodes fukuii Inoue, 1951 (developmental stage)	Inoue, 1952
Tenodera sinensis Saussure, 1871	C-Chordodes japonensis Inoue, 1952 (developmental stage)	Inoue, 1952; 1962a
Unstated sp. (Mantid)	C-Chordodes aethiopicus Inoue, 1974 (developmental stage)	Inoue, 1974
Unstated sp. (Mantids)	C-Chordodes brasiliensis Janda, 1894 (developmental stage)	Carvalho, 1946a
Unstated sp. (Mantid)	C-Chordodes capensis Camerano, 1895 (developmental stage)	Baylis, 1927
Unstated sp. (Mantid)	C-Gordionus kaschgaricus (Camerano, 1897) (developmental stage)	Inoue, 1952
Unstated sp. (Mantid)	G-Gordius sp. (developmental stage)	Pelser-Berensberg, 1909
	Family Phasmatidae	
Phybalosoma pythonis Westwood, 1859	G-Gordius aeneus Villot, 1874 [?=Gordius robustus Leidy, 1851] (developmental stage)	Römer, 1895b

Family Rhaphidophoridae
[or Gryllacrididae]

Tachycines asinamorus Adelung, 1902	C-*Gordionus alpestris* (Villot, 1884) (developmental stage)	Corbel, 1967
Troglophilus cavicola (Kollar, 1833)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Corbel, 1967

Family Tettigoniidae

Acanthodis sp.	G-*Acutogordius doriae* (Camerano, 1890) [?=*Acutogordius feae* (Camerano, 1888)] (developmental stage)	Camerano, 1892b, 1897a; Heinze, 1952; Sciacchitano, 1963
Aethiomerus adelphus Redtenbacher, 1891	C-*Pseudochordodes pardalis* (Camerano, 1893) (developmental stage)	Camerano, 1897a, 1915
Amblycorypha oblongifolia (DeGeer, 1773)	G-*Gordius robustus* Leidy, 1851 (developmental stage)	Riley *et al.*, 1878
Anabrus simplex Haldeman, 1852	G-*Gordius robustus* Leidy, 1851 (developmental stage)	La Rivers, 1949; Riley *et al.*, 1878; Thorne, 1940; Wakeland, 1959
Antaxius pedestris (Fabricius, 1787)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Camerano, 1915; Diesing, 1851; Linstow, 1878
Barbitistes serricauda (Fabricius, 1794)	G-*Gordius barbitistis-serricaudae* Diesing, 1851 (developmental stage)	Diesing, 1851; Siebold, 1843; Linstow, 1878
Ceuthophilus sp.	Unstated sp. Gordioidea (developmental stage)	Montgomery, 1899
Decticus sp.	C-*Chordodes joyeuxi* Dorier, 1935 (developmental stage)	Houdemer, 1938

Decticus sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Mrazek, 1926
Decticus albifrons (Fabricius, 1775) [=Tettigonia albifrons]	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1930, 1965
Decticus albifrons (Fabricius, 1775) [=Tettigonia albifrons]	C-Paragordius stylosus (Linstow, 1883) (developmental stage)	Heinze, 1937, 1941
Decticus albifrons (Fabricius, 1775) [=Tettigonia albifrons]	C-Paragordius tricuspidatus (Dufour, 1828) (developmental stage)	Blunck, 1922; Camerano, 1915; Heinze, 1941
Decticus verrucivorus (Linnaeus, 1758) [=Tettigonia verrucivorus]	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Deronde, 1936; Weiser, 1966
Decticus verrucivorus (Linnaeus, 1758) [=Tettigonia verrucivorus]	G-Gordius dectici Heinze, 1937 (developmental stage)	Heinze, 1937, 1941
Deracantha onos (Pallas, 1772)	G-Gordius sp. (developmental stage)	Siebold, 1854
Ephippiger ephippiger Fiebig, 1784	G-Gordius sp. (developmental stage)	Dorier, 1930
Ephippiger perforatus (Rossi, 1790) [=Rossius]	G-Gordius barbitistis-perforati Diesing, 1851 (developmental stage)	Diesing, 1851
Ephippiger provincialis (Yersin, 1854)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1930
Hexacentrus japonicus Karny (date?)	C-Chordodes japonensis Inoue, 1952 (developmental stage)	Inoue, 1955

Meroncidius glabratus (Burmeister, 1838)	C-*Chordodes parasitus* Creplin, 1847 [=*Gordius chordodes* Diesing, 1851] (developmental stage)	Camerano, 1915; Linstow, 1878; Montgomery, 1898a
Metrioptera brachyptera (Linnaeus, 1761)	G-*Gordius* sp. (developmental stage)	Ebner, 1940; Wülker, 1964
Microcentrum sp.	C-*Chordodes lichyi* Scorza, 1952 (developmental stage)	Scorza, 1952
Onconotus laxmanni (Pallas, 1771)	G-*Gordius bradipori-laxmanni* Diesing, 1851 (developmental stage)	Diesing, 1851
Ontonotus onus (*auct.*?)(*nomen nudum*) [?=*Deracantha onos* (Pallas, 1772)] *or* [?=*Saga pedo* (Pallas, 1771)]	G-*Gordius annulatus* Linstow, 1906 [?=*Gordius aquaticus* Linnaeus, 1758] (developmental stage)	Linstow, 1906c
Orchelimum sp.	G-*Gordius* sp. (developmental stage)	Walsh and Riley, 1869
Orchelimum glaberrimum (Burmeister, 1838)	G-*Gordius robustus* Leidy, 1851 (developmental stage)	Riley, *et al.*, 1878
Orchelimum gladiator Brunner, 1891	Unstated sp. Gordioidea (developmental stage)	Morris *et al.*, 1975
Orchelimum gracile Harris, 1841	G-*Gordius robustus* Leidy, 1851 (developmental stage)	Riley *et al.*, 1878; Thorne, 1940; Walsh and Riley, 1868
Orchelimum validum (Walker, 1869) [=*Orchelimum nigripes* Scudder, 1875]	G-*Gordius robustus* Leidy, 1851 (developmental stage)	May, 1919

Orchelimum vulgare Harris, 1841	G-Gordius robustus Leidy, 1851 (developmental stage)	May, 1919; Thorne, 1940
Pholidoptera sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915 Linstow, 1898
Pholidoptera sp.	C-Paragordius sp. (developmental stage)	Ebner, 1940; Wülker, 1964
Pholidoptera aptera (Fabricius, 1793)	G-Gordius hispidus Linstow, 1906 (developmental stage)	Linstow, 1906c
Saga natoliae Serville, 1839	G-Gordius sagae-natoliae Diesing, 1851 (developmental stage)	Diesing, 1851
Scudderia furcata Brunner, 1878	G-Gordius robustus Leidy, 1851 (developmental stage)	May, 1919; Thorne, 1940
Spalacomimus aberrans (Schulthess-Rechberg and Schulthess Schindler, 1898)	C-Chordodes pollonerae Camerano, 1912 (developmental stage)	Camerano, 1915
Tettigonia cantans (Fuessly, 1775)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Linstow, 1898
Tettigonia viridissima (Linnaeus, 1758) [Some taxonomists do not place parentheses about the author's name.]	G-Gordius sp. (developmental stage)	Chavannes, 1864
Tettigonia viridissima (Linnaeus, 1758)	G-Gordius albopunctatus Müller, 1926 (developmental stage)	Dorier, 1947
Tettigonia viridissima (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Camerano, 1915; Jolivet, 1946
Tettigonia viridissima (Linnaeus, 1758)	G-Gordius locustae Havlík, 1954 (developmental stage)	Havlík, 1954

<u>Xiphidium</u> <u>fasciatum</u> (DeGeer, 1773) [=<u>Conocephalus</u> <u>fasciatus</u>]	C-<u>Paragordius</u> <u>varius</u> (Leidy, 1851) (developmental stage)	May, 1919
<u>Xiphidium</u> <u>nemorale</u> Scudder, 1875 [=<u>Conocephalus</u> <u>nemorale</u>] [=<u>Anisoptera</u> <u>nemorale</u>]	G-<u>Gordius</u> <u>robustus</u> Leidy, 1851 (developmental stage)	May, 1919 Thorne, 1940
Unstated sp.	G-<u>Gordius</u> <u>robustus</u> Leidy, 1851 (developmental stage)	Ward, 1918
	Unstated family(ies)	
Unstated sp.	C-<u>Chordodes</u> <u>albibarbatus</u> Montgomery, 1898 (developmental stage)	Montgomery, 1898c
Unstated sp. (cricket)	G-<u>Gordius</u> sp. (developmental stage)	Sanford, 1856
Unstated sp. (grasshopper)	G-<u>Gordius</u> sp. (developmental stage)	Leidy, 1853
Unstated sp.	G-<u>Gordius</u> spp. (developmental stage)	Rees, 1973; Storer, 1943
Unstated sp. (grasshopper)	G-<u>Gordius</u> <u>aquaticus</u> Linnaeus, 1758 (developmental stage)	Kirtland, 1844
Unstated sp. (grasshopper)	G-<u>Gordius</u> <u>aquaticus</u> Linnaeus, 1758 (developmental stage)	Maxwell, 1908
Unstated sp. (grasshopper)	G-<u>Gordius</u> <u>horsti</u> Camerano, 1895 (developmental stage)	Inoue, 1952
Unstated sp. (grasshopper)	G-<u>Gordius</u> <u>robustus</u> Leidy, 1851 (developmental stage)	Leidy, 1851c
Unstated sp.	G-<u>Gordius</u> <u>robustus</u> Leidy, 1851 (developmental stage)	Rees, 1973; Storer, 1943

Unstated sp. (grasshopper)	C-*Neochordodes occidentalis* (Montgomery, 1898) (developmental stage)	Montgomery, 1900
	Order Dermaptera Family Forficulidae	
Chelidurella acanthopygia (Gené, 1832)	C-*Parachordodes gemmatus* (Villot, 1884) (developmental stage)	Dorier, 1930
Forficula sp.	C-*Neochordodes weberi* (Villot, 1891) (developmental stage)	Sciacchitano, 1958
Forficula auricularia Linnaeus, 1758	C-*Gordionus violaceus* (Baird, 1853) (developmental stage)	Baylis, 1944
Forficula auricularia Linnaeus, 1758	G-*Gordius forficulae-auriculariae* Diesing, 1851 (developmental stage)	Diesing, 1851
Forficula auricularia Linnaeus, 1758	G-*Gordius forficulae-borealis* Diesing, 1851 (developmental stage)	Diesing, 1851
	Unstated family	
Unstated sp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Paxton, 1844
	Order Plecoptera Family Perlidae	
Perla sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930
	Order Hemiptera Suborder Cryptocerata Family Corixidae	
Corixa striata (Linnaeus, 1758)	G-*Gordius corixae-striatae* Diesing, 1851 (developmental stage)	Ball, 1846; Diesing, 1851

Sigara sp.	C-Paragordius sp. (developmental stage)	White, 1966
	Suborder Gymnocerata Family Pentatomidae	
Pentatoma sp.	G-Gordius sp. (developmental stage)	Linstow, 1878
Pentatoma verbasci (DeGeer, 1773) [=Dolycoris baccarum (Linnaeus, 1758)]	G-Gordius sp. (developmental stage)	Villot, 1884a
	Order Homoptera Suborder Auchenorhyncha Family Cercopidae [or Aphrophoridae]	
Aphrophora spumaria Linnaeus, 1758 [=Philaenus leucoph- thalmus var. spumarius] [=Philaenus spumarius]	G-Gordius aphrophorae- spumariae Diesing, 1851 (developmental stage)	Diesing, 1851
Aphrophora spumaria Linnaeus, 1758 [=Philaenus leucoph- thalmus var. spumarius] [=Philaenus spumarius]	G-Gordius locustarum Oken, 1815 [?=Gordius locustinae Diesing, 1851] (developmental stage)	Polozhentsev, 1954; Stiles and Hassall, 1920
Cercopis sp.	G-Gordius locustarum Oken, 1815 [?=Gordius locustinae Diesing, 1851] (developmental stage)	Stiles and Hassall, 1920; Van Zwaluwen- burg, 1928
	Suborder Sternorhyncha Family Chermidae [=Adelgidae] [=Aphidae]	
Chermes abietis Linnaeus, 1758 [=Adelges abietis]	G-Gordius aphidis-gallarum- abietis Diesing, 1851 (developmental stage)	Diesing, 1851

	Family Coccidae	
Coccus sp.	G-Gordius cocci Diesing, 1851 (developmental stage)	Diesing, 1851
	Order Neuroptera Family Sialidae	
Sialis lutaria (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Dorier, 1930; Linstow, 1891a
Unstated sp.	G-Gordius sp. (developmental stage)	Mellanby, 1951
	Order Trichoptera Family Brachycentridae	
Brachycentrus sp.	C-Paragordius sp. (developmental stage)	White, 1969
	Family Limnephilidae	
Chaetopteryx sp.	G-Gordius setiger Schneider, 1866 (developmental stage)	Heinze, 1936
Limnephilus griseus (Linnaeus, 1758)	G-Gordius phryganeae-griseae Diesing, 1851 (developmental stage)	Diesing, 1851
Limnephilus rhombicus (Linnaeus, 1758)	G-Gordius spp. (developmental stage)	Linstow, 1898
Limnephilus rhombicus (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Linstow, 1898
Limnephilus vittatus (Fabricius, 1798)	G-Gordius setiger Schneider, 1866 (developmental stage)	Heinze, 1937, 1941
Potamophylax latipennis (Curtis, 1834)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Linstow, 1898, 1906a

Potamophylax stellatus (Curtis, 1834)	G-*Gordius albopunctatus* Müller, 1926 (developmental stage)	Heinze, 1937, 1941
Stenophylax sp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Dorier, 1925, 1930
Unstated sp.	G-*Gordius albopunctatus* Müller, 1926 (developmental stage)	Heinze, 1937, 1941
Unstated sp.	G-*Gordius setiger* Schneider, 1866	Heinze, 1937, 1941
	Family Phryganeidae	
Phryganea sp.	G-*Gordius* sp. (cystic stage)	Balduf, 1939; Siltala, 1906
Phryganea sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Meissner, 1856
Phryganea sp. [Both adult and larval forms.]	G-*Gordius phryganeae* Diesing, 1851 (developmental stage)	Diesing, 1851; Linstow, 1878
Phryganea sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Blunck, 1922; Dorier, 1930
Phryganea grandis Linnaeus, 1758	G-*Gordius* sp. (developmental stage)	Balduf, 1939; Dorier, 1930
	Family Rhyacophilidae	
Agapetus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930
Rhyacophila nubila (Zetterstedt, 1840)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Dorier, 1930; Linstow, 1906a
Rhyacophila obliterata McLachlan, 1863	G-*Gordius* sp. (cystic stage)	Balduf, 1939; Dorier, 1930

	Order Lepidoptera Suborder Monotrysia [or Jugatae] Family Hepialidae	
Hepialus humuli humuli (Linnaeus, 1758)	G-*Gordius hepioli-humuli* Diesing, 1851 (developmental stage)	Diesing, 1851
Hepialus humuli humuli (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Assmuss, 1858; Schultz, 1900
	Suborder Ditrysia [or Frenatae] Family Arctiidae	
Arctia caja (Linnaeus, 1758)	G-*Gordius euprepiae-cajae* Diesing, 1851 [=*Gordius erucarum* Werner, 1782] (developmental stage)	Diesing, 1851; Dujardin, 1845
Tyria jacobaeae (Linnaeus, 1758)	G-*Gordius euprepiae-jacobaeae* [?=*Gordius erucarum* Werner, 1782] (developmental stage)	Diesing, 1851; Schultz, 1900; Van Zwaluwenburg, 1928
	Family Danaidae	
Danaus chrysippus (Linnaeus, 1758) [Some taxonomists do not place parentheses about the author's name.]	G-*Gordius* sp. (developmental stage)	Pelser-Berensberg, 1909
	Family Drepanidae	
Drepana falcataria falcataria (Linnaeus, 1758)	G-*Gordius platyptericis-falculae* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Elachistidae	
Elachista argentella (Clerck, 1759)	G-*Gordius elachistae-cygnipenellae* Diesing, 1851 (developmental stage)	Diesing, 1851

Family Geometridae

Abraxas grossulariata (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Assmuss, 1858; Schultz, 1900
Cabera pusaria (Linnaeus, 1758)	Unstated sp. Gordioidea (developmental stage)	Schultz, 1900
Hydriomena furcata (Thunberg, 1784)	G-Gordius sp. (developmental stage)	Schultz, 1900
Opisthograptis luteolata (Linnaeus, 1758)	G-Gordius ennomi-crataegatae Diesing, 1851 (developmental stage)	Diesing, 1851
Scotorythra paludicola (Butler, 1879)	G-Gordius sp. (developmental stage)	Van Zwaluwenburg, 1928
Scotorythra rara (Butler, 1879)	G-Gordius sp. (developmental stage)	Van Zwaluwenburg, 1928

Family Lasiocampidae

Gastropacha quercifolia (Linnaeus, 1758)	G-Gordius gastropachae-quercifoliae Diesing, 1851 [?=Gordius erucarum Werner, 1782] (developmental stage)	Diesing, 1851; Van Zwaluwenburg, 1928
Lasiocampa quercus (Linnaeus, 1758)	G-Gordius gastropachae-quercus Diesing, 1851 [=Gordius erucarum Werner, 1782] (developmental stage)	Diesing, 1851; Dujardin, 1845; Werner, 1782
Lasiocampa trifolii (Denis and Schiffermüller, 1775)	G-Gordius gastropachae-trifolii Diesing, 1851 (developmental stage)	Diesing, 1851

Family Lycaenidae

Quercusia quercus (Linnaeus, 1758)	G-Gordius lycaenae-quercus Diesing, 1851 [=Gordius erucarum Werner, 1782] (developmental stage)	Diesing, 1851; Werner, 1782

Thecla betulae (Linnaeus, 1758)	G-*Gordius lycaenae-betulae* Diesing, 1851 [=*Gordius erucarum* Werner, 1782] (developmental stage)	Diesing, 1851 Werner, 1782
	Family Lymantriidae [=Liparidae]	
Leucoma salicis (Linnaeus, 1758)	G-*Gordius liparidis-salicis* Diesing, 1851 (developmental stage)	Diesing, 1851
Lymantria dispar (Linnaeus, 1758)	G-*Gordius liparidis-disparis* Diesing, 1851 (developmental stage)	Diesing, 1851
Lymantria monacha (Linnaeus, 1758)	G-*Gordius liparidis-monachae* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Noctuidae	
Abrostola triplasia (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Assmuss, 1858; Schultz, 1900
Agrotis sp.	G-*Gordius* sp. (developmental stage)	Pelser-Berensberg, 1909
Agrotis ripae (Hübner, 1823)	G-*Gordius agrotidis-ripae* Diesing, 1851 (developmental stage)	Diesing, 1851
Autographa gamma (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858; Schultz, 1900
Catocala fraxini (Linnaeus, 1758)	G-*Gordius catocalae-fraxini* Diesing, 1851 (developmental stage)	Diesing, 1851; Schultz, 1900
Catocala nupta (Linnaeus, 1767)	G-? *Gordius acuminatus* (Rudolphi, 1809) (developmental stage)	Oken, 1815; Rudolphi, 1809
Cucullia artemisiae (Hufnagel, 1766)	G-*Gordius* sp. (developmental stage)	Siebold, 1854

Cucullia scrophulariae (Denis and Schiffermüller, 1775)	G-Gordius sp. (developmental stage)	Fiedler, 1909
Dichonia aprilina (Linnaeus, 1758)	G-Gordius miseliae-aprilinae Diesing, 1851 (developmental stage)	Diesing, 1851
Naenia typica (Linnaeus, 1758)	G-Gordius noctuae-typicae Diesing, 1851 (developmental stage)	Diesing, 1851; Schultz, 1900
Periphanes delphinii (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Schultz, 1900
Scoliopteryx libatrix (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Assmuss, 1858; Schultz, 1900
	Family Notodontidae	
Cerura vinula (Linnaeus, 1758)	G-Gordius sp. (developmental stage)	Schultz, 1900
Eligmodonta ziczac (Linnaeus, 1758)	G-Gordius notodontae-ziczac Diesing, 1851 (developmental stage)	Diesing, 1851
Ptilodon camelina (Linnaeus, 1758)	G-Gordius notodontae-camelinae Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Nymphalidae	
Aglais urticae (Linnaeus, 1758)	G-Gordius sp. (developmental stage)	Slevogt, 1909
Aglais urticae (Linnaeus, 1758)	G-Gordius vanessae-urticae Diesing, 1851 [=Gordius erucarum Werner, 1782] (developmental stage)	Diesing, 1851 Dujardin, 1845; Werner, 1782
Aglais urticae (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Assmuss, 1858

Inachis io (Linnaeus, 1758)	G-*Gordius* sp. (developmental stage)	Slevogt, 1909
Nymphalis antiopa (Linnaeus, 1758)	G-*Gordius vanessae-antiopae* Diesing, 1851 (developmental stage)	Diesing, 1851
Nymphalis polychloros (Linnaeus, 1758)	G-*Gordius vanessae-polychlori* Diesing, 1851 [=*Gordius erucarum* Werner, 1782] [=*Gordius insectorum* Schrank, 1776] (developmental stage)	Diesing, 1851; Dujardin, 1845; Werner, 1782
	Family Papilionidae	
Papilio sp.	G-*Gordius papilionis* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Pyralididae [=Pyralidae] [=Pyraustidae]	
Eurrhypara hortulata (Linnaeus, 1758)	G-*Gordius eurrhyparae-urticatae* Baird, 1853 (developmental stage)	Baird, 1853a
	Family Saturniidae	
Actias artemis (Bremer, 1861)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Römer, 1895b
Saturnia sp.	G-*Gordius longissimus* Römer, 1895 (developmental stage)	Camerano, 1897a; Römer, 1895b
Saturnia pyri (Schiffermüller, 1776)	G-*Gordius saturniae-pyri* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Satyridae	
Erebia euryale (Esper, 1777)	G-*Gordius* sp. (developmental stage)	Chapman, 1902

Pyronia tithonus (Linnaeus, 1771)	G-Gordius sp. (developmental stage)	Fowler, 1892; South, 1892
	Family Sphingidae	
Hyles euphorbiae (Linnaeus, 1758)	G-Gordius sphingis-euphorbiae Diesing, 1851 (developmental stage)	Diesing, 1851
Mimas tiliae (Linnaeus, 1758)	G-Gordius smerinthi-tiliae Diesing, 1851 (developmental stage)	Diesing, 1851
Sphinx ligustri Linnaeus, 1758	G-Gordius sphingis-ligustri Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Tortricidae	
Cydia pomonella (Linnaeus, 1758)	Unstated sp. Gordioidea (developmental stage)	Froggatt, 1908, cited in Stiles and Hassall, 1920
	Family Yponomeutidae	
Yponomeuta padella (Linnaeus, 1758)	G-? Gordius truncatus (Rudolphi, 1809) (developmental stage)	Oken, 1815; Rudolphi, 1809; Siebold, 1842
	Family Zygaenidae [=Pyromorphidae]	
Zygaena filipendulae (Linnaeus, 1758) [=Zygaena filipendulae filipendulae]	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Assmuss, 1858; Schultz, 1900
	Unstated family(ies)	
? Erucarum sp.	G-Gordius erucarum Werner, 1782 [?=Gordius erucarum Diesing, 1851] (developmental stage)	Diesing, 1851; Siebold, 1842; Van Zwaluwenburg, 1928; Werner, 1782

Unstated sp.	G-*Gordius larvarum* Bruguiere, 1791 (developmental stage)	Bruguiere, 1791a, *circa* 1791b, 1827; Stiles and Hassall, 1920
	Order Diptera Suborder Nematocera Family Chaoboridae [=Corethridae]	
Chaoborus sp. [=*Corethra* sp.]	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Villot, 1891
Chaoborus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Dorier, 1930; Villot, 1874, 1891
Chaoborus sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Van Zwaluwenburg, 1928
Chaoborus sp.	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Blunck, 1922; Villot, 1891
	Family Chironomidae [=Tendipedidae]	
Chironomus sp.	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Villot, 1891
Chironomus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage, with and without melanization)	Dorier, 1930; Villot, 1874, 1891
Chironomus sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Dorier, 1930; Stiles and Hassall, 1920
Chironomus sp.	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Blunck, 1922; Villot, 1891

Chironomus dorsalis Meigen, 1818	C-Chordodes japonensis Inoue, 1952 (cystic stage with melanization)	Inoue, 1960a, 1962a
Chironomus plumosus (Linnaeus, 1758)	G-Gordius chironomi-plumosi Diesing, 1851 (developmental stage)	Diesing, 1851
Tanypus sp.	C-Gordionus violaceus (Baird, 1853) (cystic stage)	Blunck, 1922; Villot, 1891
Tanypus sp.	G-Gordius aquaticus Linnaeus, 1758 (cystic stage)	Blunck, 1922; Villot, 1891
Tanypus sp.	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Dorier, 1930; Van Zwaluwenburg, 1928
Tanypus sp.	C-Paragordius tricuspidatus (Dufour, 1828) (cystic stage)	Blunck, 1922; Villot, 1891
Tanytarsus sp. [=Calopsectra sp.]	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Dorier, 1930; Švábeník, 1925
Unstated sp. (of Subfamily Orthocladiinae) [=Hydrobaeninae]	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Dorier, 1930
	Family Culicidae	
Aedes aegypti (Linnaeus, 1762)	G-Gordius robustus Leidy, 1851 (larval form, melanized)	Present author, in this dissertation
Aedes sierrensis (Ludlow, 1905)	G-Gordius robustus Leidy, 1851 (larval form, melanized)	Present author, in this dissertation
Culex sp.	C-Paragordius varius (Leidy, 1851) (cystic stage)	Montgomery, 1904

Culex pipiens Linnaeus, 1758	G-*Gordius robustus* Leidy, 1851 (larval form, melanized)	Present author, in this dissertation
Culex pipiens Linnaeus, 1758	C-*Neochordodes occidentalis* (Montgomery, 1898) (cystic stage; larval form, melanized)	Poinar and Doelman, 1974
Culex pipiens pallens Coquillett, 1898	C-*Chordodes japonensis* Inoue, 1952 (cystic stage)	Inoue, 1960a, 1962a
Culex tarsalis Coquillett, 1894	G-*Gordius robustus* Leidy, 1851 (larval form, melanized)	Present author, in this dissertation
	Family Simuliidae	
Simulium spp.	C-*Paragordius* sp. (developmental stage)	White, 1969
	Family Tipulidae	
Dicranota sp.	G-*Gordius* sp. (? developmental stage)	Bodenheimer, 1923; Van Zwaluwenburg, 1928
Dicranota sp.	C-*Parachordodes tolosanus* (Dujardin, 1920) (cystic stage)	Müller, 1920
Pedicia (*Tricyphonia*) sp.	G-*Gordius* sp. (cystic stage)	Müller, 1926
Pedicia rivosa (Linnaeus, 1758)	G-*Gordius* sp. (cystic stage)	Müller, 1926
Pedicia rivosa (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Müller, 1926
Tipula gigantea Schrank, 1776	G-*Gordius* sp. (cystic stage)	Müller, 1926

	Suborder Brachycera Family Tabanidae	
Tabanus astutus Osten Sacken, 1874	G-? *Gordius* sp. [or a nematode] (developmental stage)	Marchand, 1920, in Jenkins, 1964
Tabanus bromius Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858
	Order Coleoptera Family Brachyceridae	
Brachycerus undatus Fabricius, 1798	G-*Gordius brachyceri-undati* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Buprestidae	
Buprestis sp.	G-*Gordius buprestidis* Diesing, 1851 [=*Gordius buprestis* Rudolphi, 1809] (developmental stage)	Diesing, 1851
	Family Carabidae	
Abax parallelepipedus (Piller and Mitter- pacher, 1783)	G-*Gordius feroniae-striolae* Diesing, 1851 (developmental stage)	Diesing, 1851
Aechmites terricola (Herbst, 1783)	G-*Gordius pristonychi-* *terricolae* Diesing, 1851 (developmental stage)	Diesing, 1851
Amara sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Linstow, 1891a, 1891b; Van Zwaluwen- burg, 1928
Amara brunnea (Gyllenhal, 1810)	C-*Gordionus brunneus* Montén, 1951 (developmental stage)	Montén, 1951
Amara fusca Dejean, 1828	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Blunck, 1922; Diesing, 1861 Linstow, 1878

Amara similata (Gyllenhal, 1810)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Diesing, 1861; Linstow, 1878
Anisodactylus binotatus (Fabricius, 1787)	G-Gordius harpali-binotati Diesing, 1851 (developmental stage)	Diesing, 1851
Calathus sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Linstow, 1878
Calathus sp.	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Dorier, 1930; Švábeník, 1925
Calathus ambiguus (Paykull, 1790)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Linstow, 1889
Calathus fuscipes (Goeze, 1777)	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Camerano, 1915
Calathus fuscipes (Goeze, 1777)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915
Calathus fuscipes (Goeze, 1777)	G-Gordius calathi-cisteloidis Diesing, 1851 (developmental stage)	Diesing, 1851
Calathus fuscipes (Goeze, 1777)	C-Parachordodes pustulosus (Baird, 1853) (developmental stage)	Baylis, 1944
Calathus fuscipes (Goeze, 1777)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Heinze, 1941
Calathus stephensii (auct.?) (nomen nudum?)	G-Gordius calathi-stephensii Diesing, 1851 (developmental stage)	Diesing, 1851
Calosoma (Charmosta) maderae (Fabricius, 1775)	? C-Dacochordodes bacescui Cǎpuse, 1965 (developmental stage)	Cǎpuse, 1970

Carabus spp.	C-*Gordionus violaceus* (Baird, 1853) (developmental stage)	Baylis, 1944
Carabus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Blunck, 1922; Dorier, 1930; Mrazek, 1926; Rolleston, 1888
Carabus sp.	G-*Gordius coleopterorum* (Rudolphi, 1809) (developmental stage)	Diesing, 1851 Oken, 1815
Carabus sp.	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Villot, 1886
Carabus catenulatus Scopoli, 1763	G-*Gordius carabi-catenulati* Diesing, 1851 (developmental stage)	Diesing, 1851
Carabus coriaceus Linnaeus, 1758	C-*Gordionus sulcatus* Müller, 1926 (developmental stage)	Heinze, 1937, 1941
Carabus coriaceus Linnaeus, 1758	C-*Gordionus violaceus* (Baird, 1853) (developmental stage)	Dorier, 1930, 1965; Linstow, 1889
Carabus coriaceus Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915; Diesing, 1851
Carabus coriaceus Linnaeus, 1758	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Carabus hortensis Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915
Carabus hortensis Linnaeus, 1758	G-*Gordius carabi-hortensis* Diesing, 1851 (developmental stage)	Diesing, 1851
Carabus hortensis Linnaeus, 1758	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915

Carabus monilis Fabricius, 1792	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Villot, 1891
Carabus monilis Fabricius, 1792	G-Gordius carabi-monilis Diesing, 1851 (developmental stage)	Diesing, 1851
Carabus morbillosus Fabricius, 1792	G-Gordius carabi-alternantis Diesing, 1851 (developmental stage)	Diesing, 1851
Carabus morbillosus Fabricius, 1792	G-Gordius carabi-morbillosi Diesing, 1851 (developmental stage)	Diesing, 1851
Carabus morbillosus Fabricius, 1792	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Camerano, 1915; Linstow, 1898
Carabus olyosidus Illig. (nomen nudum?) (auct.? and date?)	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Camerano, 1915
Carabus smaragdinus Fischer von Waldheim, 1824	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Römer, 1895b
Carabus ulrichi Germar, 1824	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Linstow, 1898
Carabus violaceus Linnaeus, 1758	C-Gordionus violaceus (Baird, 1853) [=Gordius carabi-violacei Diesing, 1851] (developmental stage)	Camerano, 1915; Diesing, 1851, 1861; Van Zwaluwenburg, 1928
Carabus violaceus Linnaeus, 1758	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915
Carabus violaceus Linnaeus, 1758	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Cychrus caraboides (Linnaeus, 1758)	G-Gordius cychri-rostrati Diesing, 1851 (developmental stage)	Diesing, 1851

Cymindis humeralis (Fourcroy, 1785)	G-Gordius cymindis-humeralis Diesing, 1851 (developmental stage)	Diesing, 1851
Dolichus halensis (Schaller, 1783)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Assmuss, 1858
Harpalus spp.	G-Gordius spp. (developmental stage)	Hausman, 1923
Harpalus sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Linstow, 1883a; Mrazek, 1926
Harpalus sp.	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Linstow, 1891a,1891b
Harpalus aenus var. azureus Panzer, 1801	G-Gordius harpali-azurei Diesing, 1851 (developmental stage)	Diesing, 1851
Harpalus affinis (Schrank, 1781)	C-Gordionus harpali Heinze, 1940 (developmental stage)	Heinze, 1941
Harpalus affinis (Schrank, 1781)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Dorier, 1930
Harpalus affinis (Schrank, 1781)	G-Gordius harpali-aenei Diesing, 1851 (developmental stage)	Diesing, 1851
Harpalus affinis (Schrank, 1781)	C-Parachordodes pustulosus (Baird, 1853) (developmental stage)	Blunck, 1922; Camerano, 1892d, 1915
Harpalus atratus (Duftschmid, 1812)	G-Gordius sp. (developmental stage)	Gemminger, 1849
Harpalus atratus (Duftschmid, 1812)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Linstow, 1898
Harpalus cephalotes Fairmaire and Laboulbéne, 1854-1856	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Heinze, 1937, 1941

Harpalus distinguendus (Duftschmid, 1812)	C-Parachordodes speciosus (Janda, 1894) (developmental stage)	Heinze, 1937, 1941
Harpalus hirtipes (Panzer, 1797)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Linstow, 1898
Harpalus hospes Sturm, 1818	Unstated sp. (developmental stage)	Siebold, 1858
Harpalus oblitus Dejean, 1829	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915
Harpalus rufipes (DeGeer, 1774)	G-Gordius spp. (developmental stage)	Siebold, 1854
Harpalus rufipes (DeGeer, 1774)	G-Gordius harpali-ruficornis Diesing, 1851 (developmental stage)	Diesing, 1851
Harpalus rufipes (DeGeer, 1774)	C-Parachordodes gemmatus (Villot, 1884) (developmental stage)	Heinze, 1937, 1941
Harpalus rufipes (DeGeer, 1774)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930
Lesticus magnus (von Motschulsky, 1860)	C-Parachordodes lestici Heinze, 1935 (developmental stage)	Heinze, 1935b
Lorocera caerulescens (Linnaeus, 1758) [=Pterostichus caeru- lescens]	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Assmuss, 1858
Molops depressus Parreyss, 1826	G-Gordius sp. (developmental stage)	Gemminger, 1849
Molops elatus (Fabricius, 1801)	G-Gordius sp. (developmental stage)	Gemminger, 1849
Molops elatus (Fabricius, 1801)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915 Heinze, 1941

Molops piceus (Panzer, 1793)	C-Gordionus molopsis Heinze, 1937 (developmental stage)	Heinze, 1937, 1941
Molops piceus (Panzer, 1793)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Brightwell, 1835
Molops piceus var. austriacus Ganglbauer, 1889 [=Molops piceus (Panzer, 1793)]	C-Gordionus wolterstorffii (Camerano, 1888) (developmental stage)	Heinze, 1941
Nebria picicornis (Fabricius, 1801)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Müller, 1920
Oregus aereus (White, 1846)	Unstated sp. Gordioidea (developmental stage)	Townsend, 1970
Pterostichus sp.	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Sciacchitano, 1933
Pterostichus sp.	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Mrazek, 1926
Pterostichus sp.	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Dorier, 1930; Švábeník, 1925
Pterostichus burmeisteri Heer, 1841	G-Gordius feroniae-metallicae Diesing, 1851 (developmental stage)	Diesing, 1851
Pterostichus burmeisteri Heer, 1841	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Pterostichus burmeisteri Heer, 1841	C-Paragordionus dispar Müller, 1926 (developmental stage)	Heinze, 1937, 1941
Pterostichus cupreus (Linnaeus, 1758)	G-Gordius poecili-cuprei Diesing, 1851 (developmental stage)	Diesing, 1851

Pterostichus honestus Say, 1825	G-Gordius robustus Leidy, 1851 (developmental stage)	Leidy, 1856; Villot, 1874
Pterostichus lepidus (Leske, 1785)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Gemminger, 1849
Pterostichus lepidus (Leske, 1785)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Pterostichus madidus (Fabricius, 1775)	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Baylis, 1944; Dollfus, 1944; Jolivet, 1944a, 1944b
Pterostichus madidus (Fabricius, 1775)	C-Gordionus wolterstorffii (Camerano, 1888) (developmental stage)	Baylis, 1944
Pterostichus madidus (Fabricius, 1775)	G-Gordius sp. [or a filarial nematode] (developmental stage)	Brightwell, 1835
Pterostichus madidus (Fabricius, 1775)	G-Gordius spp. (developmental stage)	Jolivet, 1944b
Pterostichus madidus (Fabricius, 1775)	G-Gordius feroniae-madidae Diesing, 1851 (developmental stage)	Diesing, 1851
Pterostichus madidus (Fabricius, 1775)	C-Parachordodes pustulosus (Baird, 1853) (developmental stage)	Baylis, 1944
Pterostichus melas (Creutzer, 1799)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Camerano, 1915
Pterostichus melas (Creutzer, 1799)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Heinze, 1941
Pterostichus niger (Schaller, 1783)	C-Gordionus scaber hykai Havlik, 1947 (developmental stage)	Havlik, 1947

<u>Pterostichus</u> <u>niger</u> (Schaller, 1783)	C-<u>Gordionus</u> <u>scaber</u> <u>scaber</u> Müller, 1926 (developmental stage)	Havlik, 1947
<u>Pterostichus</u> <u>niger</u> (Schaller, 1783)	C-<u>Gordionus</u> <u>scaber</u> <u>silesiae</u> Heinze, 1937 (developmental stage)	Heinze, 1937, 1941
<u>Pterostichus</u> <u>niger</u> (Schaller, 1783)	C-<u>Parachordodes</u> <u>tolosanus</u> (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Heinze, 1941
<u>Pterostichus</u> <u>nigrita</u> (Fabricius, 1792)	G-<u>Gordius</u> <u>feroniae-omasei-nigritae</u> Diesing, 1851 (developmental stage)	Diesing, 1851
<u>Pterostichus</u> <u>nigrita</u> (Fabricius, 1792)	C-<u>Parachordodes</u> <u>tolosanus</u> (Dujardin, 1842) (developmental stage)	Camerano, 1915; Linstow, 1898
<u>Pterostichus</u> <u>ovoideus</u> Sturm, 1824 [=<u>Pterostichus</u> <u>inter-stinctus</u> Sturm, 1824]	C-<u>Gordionus</u> <u>dubiosus</u> Heinze, 1937 (developmental stage)	Căpuse, 1970
<u>Pterostichus</u> <u>vulgaris</u> (Linnaeus, 1758)	C-<u>Gordionus</u> <u>preslii</u> (Vejdovsky, 1886) (developmental stage)	Blunck, 1922; Heinze, 1937; Vejdovsky, 1894
<u>Pterostichus</u> <u>vulgaris</u> (Linnaeus, 1758)	C-<u>Gordionus</u> <u>sulcatus</u> Müller, 1926 (developmental stage)	Heinze, 1937, 1941
<u>Pterostichus</u> <u>vulgaris</u> (Linnaeus, 1758)	C-<u>Gordionus</u> <u>violaceus</u> (Baird, 1853) (developmental stage)	Dorier, 1930; Heinze, 1941
<u>Pterostichus</u> <u>vulgaris</u> (Linnaeus, 1758)	G-<u>Gordius</u> <u>aquaticus</u> Linnaeus, 1758 (developmental stage)	Camerano, 1915 Linstow, 1898; Siebold, 1858
<u>Pterostichus</u> <u>vulgaris</u> (Linnaeus, 1758)	G-<u>Gordius</u> <u>feroniae-melanariae</u> Diesing, 1851 (developmental stage)	Diesing, 1851

Pterostichus vulgaris (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915; Linstow, 1898
Sphodrus leucophthalmus (Linnaeus, 1758)	G-Gordius sp. (developmental stage)	Rosa, 1882
Sphodrus leucophthalmus (Linnaeus, 1758)	G-Gordius sphodri-leucophthalmi Diesing, 1851 (developmental stage)	Diesing, 1851
Sphodrus leucophthalmus (Linnaeus, 1758)	C-Parachordodes pustulosus (Baird, 1853) (developmental stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930
Sphodrus leucophthalmus (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Zabrus blaptoides (Creutzer, 1799) [=Zabrus blapoides]	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922
Zabrus blaptoides (Creutzer, 1799) [=Zabrus blapoides]	G-Gordius peloris-blapoidis Diesing, 1851 [=Gordius peloris-blaptoidis Linstow, 1878] (developmental stage)	Diesing, 1851; Linstow, 1878
Zabrus blaptoides (Creutzer, 1799) [=Zabrus blapoides]	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Zabrus tenebrioides (Goeze, 1777) [=Zabrus gibbus (Fabricius, 1794)]	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Blunck, 1922; Siebold, 1854
Unstated sp.	C-Parachordodes sciacchitanoi Heinze, 1935 (developmental stage)	Heinze, 1935b
Unstated sp.	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Römer, 1895b

Unstated sp. (of Tribe Broscini)	Unstated sp. Gordioidea (developmental stage)	Townsend, 1970
	Family Cerambycidae	
Hylotrupes bajulus (Linnaeus, 1758)	G-*Gordius hylotrupis-bajuli* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Chrysomelidae	
Agelastica alni (Linnaeus, 1758)	G-*Gordius gallerucae-alni* Diesing, 1851 (developmental stage)	Diesing, 1851
Galeruca tanaceti (Linnaeus, 1758) [=*Agelastica tenaceti*]	G-*Gordius gallerucae-tenaceti* Diesing, 1851 (developmental stage)	Diesing, 1851
Timarcha tenebricosa (Fabricius, 1775)	C-*Gordionus violaceus* (Baird, 1853) (developmental stage)	Dorier, 1930; Jolivet, 1948; Jolivet and Théodoridès, 1950
	Family Curculionidae	
Conotrachelus aratus (Germar, 1824)	Unstated sp. Gordioidea (developmental stage)	Brooks, 1922
Otiorrhynchus rhacusensis (Germar, 1822)	G-*Gordius otiorhynchi-ragusensis* Diesing, 1851 (developmental stage)	Diesing, 1851
	Family Dytiscidae	
Acilius sulcatus (Linnaeus, 1758)	G-*Gordius acilii-sulcati* Diesing, 1851 (developmental stage)	Diesing, 1851
Agabus brunneus (Fabricius, 1798)	G-*Gordius colymbetis-ferruginei* Diesing, 1851 (developmental stage)	Diesing, 1851 Dollfus, 1932

Colymbetes striatus (Linnaeus, 1758)	G-*Gordius colymbetis-striati* Diesing, 1851 (developmental stage)	Diesing, 1851; Dollfus, 1932
Dytiscus spp.	G-*Gordius* spp. (developmental stage)	Dujardin, 1842; Guignot, 1933; Mellanby, 1951
Dytiscus sp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Blunck, 1922; Rolleston, 1888
Dytiscus spp. [other than *Dytiscus marginalis* Linnaeus, 1758]	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Heinze, 1937
Dytiscus sp.	C-*Paragordius tricuspidatus* (Dufour, 1828) (developmental stage)	Camerano, 1915
Dytiscus (*Macrodytes*) sp.	Unstated sp. Gordioidea (developmental stage)	Filipjev and Schuurmans Stekhoven, 1941
Dytiscus marginalis Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Blunck, 1924; Dorier, 1930; Heinze, 1941
Dytiscus marginalis Linnaeus, 1758	G-*Gordius dytiscorum* Legrand, 1856 (developmental stage)	Dollfus, 1932; Legrand, 1858
Dytiscus marginalis Linnaeus, 1758	C-*Parachordodes tolosanus* (Dujardin, 1842) (developmental stage)	Blunck, 1924; Camerano, 1915 Dollfus, 1932
Dytiscus marginalis Linnaeus, 1758	C-*Paragordius tricuspidatus* (Dufour, 1828) (developmental stage)	Villot, 1891
Dytiscus (*Macrodytes*) *marginalis* Linnaeus, 1758	Unstated sp. Gordioidea (developmental stage)	Blunck, 1922; Dorier, 1965
Dytiscus semisulcatus Müller, 1776	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Heinze, 1937, 1941

Dytiscus semisulcatus Müller, 1776	Unstated sp. Gordioidea (developmental stage)	Blunck, 1922; Dollfus, 1932
	Family Hydrophilidae	
Hydrophilus spp.	G-*Gordius* spp. (developmental stage)	Dujardin, 1842
Hydrophilus sp.	G-*Gordius hydrophili* Diesing, 1851 [=*Gordius aquaticus* Linnaeus, 1758] (developmental stage)	Diesing, 1851; Linstow, 1878; Siebold, 1850
Hydrophilus piceus (Linnaeus, 1758)	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Dorier, 1930
Hydrophilus piceus (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Blunck, 1922; Dorier, 1930
Hydrophilus piceus (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Blunck, 1922 Dorier, 1930
Hydrophilus piceus (Linnaeus, 1758)	C-*Paragordius tricuspidatus* (Dufour, 1828) (cystic stage)	Blunck, 1922; Dorier, 1930
	Family Scarabaeidae	
Melolontha melolontha (Linnaeus, 1758)	G-? *Gordius* sp. (developmental stage)	Leblond, 1837; Siebold, 1843; Linstow, 1878
Oryctes nasicornis (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Assmuss, 1858
	Family Silphidae	
Silpha sp.	G-*Gordius* sp. (developmental stage)	Höfmanner, 1913
Silpha atrata Linnaeus, 1758 [=*Phosphuga atrata*]	C-*Gordionus silphae* Heinze, 1937 (developmental stage)	Heinze, 1937; 1941

Silpha atrata Linnaeus, 1758	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Camerano, 1915; Southern, 1909
Silpha atrata Linnaeus, 1758	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Camerano, 1915; Hartmeyer, 1909
Silpha atrata Linnaeus, 1758	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Camerano, 1915
Silpha carinata Herbst, 1783 [=Silpha carinata Illiger, 1798]	C-Parachordodes tolosanus (Dujardin, 1842) (developmental stage)	Blunck, 1922; Diesing, 1861; Linstow, 1906a
Silpha obscura Linnaeus, 1758	C-Gordionus violaceus (Baird, 1853) (developmental stage)	Dorier, 1930
Silpha obscura Linnaeus, 1758	C-Gordius silphae-obscurae Diesing, 1851 (developmental stage)	Diesing, 1851
Silpha tristis Illiger, 1798	C-Gordionus silphae Heinze, 1937 (developmental stage)	Heinze, 1937, 1941
	Family Staphylinidae	
Creophilus maxillosus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Assmuss, 1858
Ocypus megacephalus (von Nordmann, 1837) [Citation of above name unverified.]	G-Gordius sp. (developmental stage)	Siebold, 1858
	Family Tenebrionidae	
Blaps lethifera Marsham, 1802	C-Parachordodes pustulosus (Baird, 1853) (developmental stage)	Baird, 1853a, 1853b; Linstow, 1878; Oerley, 1881; Baylis, 1944

Blaps lusitanica Herbst, 1799	G-*Gordius blapis-productae* Diesing, 1851 (developmental stage)	Diesing, 1851; Seurat, 1916
Blaps mortisaga (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Dufour, 1837; Gervais, 1835
Blaps mortisaga (Linnaeus, 1758)	C-*Parachordodes pustulosus* (Baird, 1853) (developmental stage)	Blunck, 1922; Camerano, 1915; Heinze, 1941
Blaps mortisaga (Linnaeus, 1758)	C-*Paragordius tricuspidatus* (Dufour, 1828) [=*Gordius blapis-mortisagae* Diesing, 1851] (developmental stage)	Diesing, 1851; Dorier, 1930; Linstow, 1878; Seurat, 1916
Blaps mucronata Latreille, 1804	C-*Parachordodes pustulosus* (Baird, 1853) (developmental stage)	Blunck, 1922; Dorier, 1930
Blaps obtusa Linnaeus (*auct*.?)(date?) [?=*Blaps obtusa* Fabricius, 1798] [?=*Blaps obtusa* Sturm, 1807] *or* [?=*Blaps obtusa* Gyllenhal, 1813]	C-*Parachordodes pustulosus* (Baird, 1853) (developmental stage)	Siebold, 1858
Blaps pterotapha Fischer von Waldheim, 1832	C-*Parachordodes pustulosus* (Baird, 1853) (developmental stage)	Blunck, 1922; Camerano, 1915
Prosodes obtusa (Fabricius, 1798) [=*Blaps obtusa*]	C-*Parachordodes pustulosus* (Baird, 1853) (developmental stage)	Kiryanova, 1971
	Unstated family(ies)	
Unstated sp.	G-*Gordius* sp. (developmental stage)	Thomas and Poinar, 1973
Unstated sp.	G-*Gordius aquaticus* Linnaeus, 1758 (developmental stage)	Römer, 1895b

Order Hymenoptera
Suborder Symphyta
Family Tenthredinidae

Tenthredo sp.	G-*Gordius* *tenthredinis* (Gmelin, 1790) (developmental stage)	Diesing, 1851; Stiles and Hassall, 1920

Suborder Apocrita
Family Apidae

Apis sp. [Possibly *Apis* *mellifera* Linnaeus, 1758]	G-*Gordius* *aquaticus* Linnaeus, 1758 (developmental stage)	Cury, 1946
Apis *mellifera* Linnaeus, 1758	G-? *Gordius* sp. (developmental stage)	Linstow, 1889
Bombus sp.	G-*Gordius* *bombi* Diesing, 1851 (developmental stage)	Diesing, 1851
Bombus *terrestris* (Linnaeus, 1758)	G-*Gordius* *bombi-terrestris* Diesing, 1851 (developmental stage)	Diesing, 1851
Sphecodes *gibbus* (Linnaeus, 1758) [=*Dichroa* *gibbus*]	G-*Gordius* *sphaecodis-gibbi* Diesing, 1851 [=*Gordius* *sphaecodis* (Dufour, 1837)] (developmental stage)	Diesing, 1851; Linstow, 1878; Van Zwaluwenburg, 1928

Family Braconidae

Microgaster *glomeratus* (Linnaeus, 1758)	G-*Gordius* sp. (developmental stage)	Slevogt, 1909

Family Formicidae

Formica sp.	G-*Gordius* *formicarum* Diesing, 1851 (developmental stage)	Diesing, 1851
Technomyrmex *albipes* (F. Smith, 1861)	G-*Gordius* *formicarum* Diesing, 1851 (developmental stage)	Donisthorpe, 1927

Family Vespidae

Polistes aurifer Saussure, 1853	G-Gordius sp. (developmental stage)	Van Zwaluwenburg, 1928
Vespa crabro Linnaeus, 1758	G-Gordius vespae-crabronis Diesing, 1851 (developmental stage)	Diesing, 1851
Vespula germanica (Fabricius, 1793)	G-Gordius sp. [Probably a mermithoid worm rather than a gordiid.] (developmental stage)	Kloft, 1951; Wülker, 1964 [see also Kristof, 1878]
Vespula vulgaris (Linnaeus, 1758)	G-Gordius sp. [Probably a mermithoid worm rather than a gordiid.] (developmental stage)	Kristof, 1878
Vespula vulgaris (Linnaeus, 1758)	G-Gordius vespae-vulgaris Baird, 1853 [Probably a mermithoid worm rather than a gordiid.] (developmental stage)	Baird, 1853a; Siebold, 1858

Class Chilopoda
Order Lithobiomorpha
Family Lithobiidae

Lithobius forficatus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1929, 1930

Order Scolopendromorpha
Family Scolopendridae

Scolopendra cingulata Latreille, 1829	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1929; 1930
Scolopendra cormocephalina Kohlr. (date?)	G-Gordius robustus Leidy, 1851 (developmental stage)	Carvalho, 1946b

	Class Diplopoda	
	Order Glomerida [?=Plesiocerata] or [?=Oniscomorpha]	
	Family Glomeridae	
Glomeris humbertiana Saussure (date?)	G-Gordius sp. (developmental stage)	Dorier, 1930
Glomeris marginatus (de Villers, 1789)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage)	Dorier, 1929, 1930
	Order Polydesmida [=Polydesmoidea] or [?=Proterospermophora]	
Polydesmus complanatus (Linnaeus, 1761)	C-Gordionus alpestris (Villot, 1884) (developmental stage)	Căpuse, 1970
	Order Spirobolida	
	Family Spirobolidae	
Spirobolus sp. [=Narceus sp.]	G-Gordius sp. (developmental stage)	Cooper and Storck, 1973
	Order Julida [=Juliformia] [?=Opisthospermophora]	
	Family Iulidae [=Julidae]	
Cylindroiulus teutonicus (Pocock, 1900)	Unstated sp. Gordioidea (developmental stage)	Sahli, 1972
Iulus sp. [=Julus sp.]	C-Gordionus alpestris (Villot, 1884) (developmental stage)	Dorier, 1929, 1930
Schizophyllum sabulosum (Linnaeus, 1758) [=Ommatoiulus sabulosum]	Unstated sp. Gordioidea (developmental stage)	Sahli, 1972
Tachypodoiulus albipes (C. L. Koch, 1838)	Unstated sp. Gordioidea (developmental stage)	Sahli, 1972

Phylum Chordata
Subphylum Agnatha
Class Cyclostomata
[or Marsipobronchii]
Order Petromyzontiformes
[or Hyperoartia]
Family Petromyzonidae

Lampetra fluviatilis (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (developmental stage, in cranium)	Dorier, 1930; Freund, 1907; Linstow, 1878; Villot, 1884a
Lampetra planeri (Bloch, 1784)	C-Gordionus violaceus (Baird, 1853) (cystic stage)	Camerano, 1915; Dorier, 1930; Villot, 1891
Lampetra planeri (Bloch, 1784)	G-Gordius aquaticus Linnaeus, 1758 (cystic stage)	Camerano, 1915; Dorier, 1930; Linstow, 1898; Villot, 1891
Lampetra planeri (Bloch, 1784)	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Camerano, 1915; Dorier, 1930; Villot, 1891
Lampetra planeri (Bloch, 1784)	C-Paragordius stylosus (Linstow, 1883) (cystic stage)	Camerano, 1897a, 1915
Lampetra planeri (Bloch, 1784)	C-Paragordius tricuspidatus (Dufour, 1828) (cystic stage)	Camerano, 1915; Dorier, 1930; Villot, 1891

Subphylum Gnathostomata
Superclass Pisces

Unstated spp.	Unstated spp. Gordioidea (? adult stage, in alimentary tract)	Hoffman, 1967

Class Osteichthyes
Order Clupeiformes
Family Clupeidae

Clupea harengus Linnaeus, 1758	G-*Gordius* sp. [?=*Gordius aquaticus* Linnaeus, 1758] (? adult stage; associated with the bladder=blase)	Martin, 1771, 1775a, 1775b

Order Salmoniformes
Family Coregonidae

Coregonus wartmanni (Bloch, 1779) [=*Coregonus lavaretus* (Linnaeus, 1758)]	G-*Gordius aquaticus* Linnaeus, 1758 (? developmental stage, in alimentary tract)	Blunck, 1922; Linstow, 1883a, 1891b; Villot, 1884a

Family Salmonidae

Salmo sp.	G-*Gordius aquaticus* Linnaeus, 1758 (? developmental and adult stages, in alimentary tract)	Blunck, 1922; Diesing, 1861; Dorier, 1930; Lever, 1963
Salmo gairdneri irideus Gibbons, 1855 [or *Salmo gairdneri* Richardson, 1836]	C-*Chordodes* sp. (developmental stage, in body cavity)	Nigrelli, 1941, 1943
Salmo trutta Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (? developmental stage, in alimentary tract)	Linstow, 1883a, 1898; Villot, 1884a
Salvelinus fontinalis (Mitchill, 1815)	C-*Chordodes* sp. (developmental stage, in body cavity)	Nigrelli, 1941, 1943

Family Thymallidae

Thymallus thymallus (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage: ? developmental stage in alimentary tract)	Diesing, 1861; Linstow, 1878, 1889, 1898; Zschokke, 1884

	Order Isospondyli Family Osmeridae	
Osmerus eperlanus (Linnaeus, 1758)	G-*Gordius* sp. [?=*Gordius aquaticus* Linnaeus, 1758] (? adult stage; associated with the bladder=blase)	Martin, 1771, 1775a, 1775b
	Order Heterognathi Family Hemiodontidae	
Poecilobrycon sp.	C-*Chordodes* sp. (developmental stage, in body cavity)	Nigrelli, 1941, 1943
	Order Ostariophysi Family Cobitidae	
Misgurnus fossilis (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (? developmental stage, in cranium)	Freund, 1907; Linstow, 1889; Villot, 1884a
Nemacheilus barbatulus (Linnaeus, 1758)	C-*Gordionus violaceus* (Baird, 1853) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930
Nemacheilus barbatulus (Linnaeus, 1758)	G-*Gordius* sp. (cystic stage; ? adult stage in alimentary tract)	Kaletskaia, 1960; Linstow, 1883a; Sauvonsaari, 1971
Nemacheilus barbatulus (Linnaeus, 1758)	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage)	Blunck, 1922; Camerano, 1915; Linstow, 1898; Villot, 1891
Nemacheilus barbatulus (Linnaeus, 1758)	C-*Parachordodes tolosanus* (Dujardin, 1842) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Villot, 1891
Nemacheilus barbatulus (Linnaeus, 1758)	C-*Paragordius stylosus* (Linstow, 1883) (cystic stage)	Camerano, 1897a, 1915

Nemacheilus barbatulus (Linnaeus, 1758)	C-Paragordius tricuspidatus (Dufour, 1828) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Villot, 1891
	Family Cyprinidae	
Abramis brama (Linnaeus, 1758)	G-Gordius sp. (? developmental stage, in alimentary tract)	Blunck, 1922; Dorier, 1930; Linstow, 1891b
Aspius aspius (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (? developmental stage, in alimentary tract)	Blunck, 1922; Linstow, 1883a, 1891b, 1898; Villot, 1884a
Barbus barbus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (? adult stage, in alimentary tract)	Reichenbach-Klinke, 1962
Leuciscus (Idus) idus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (? adult stage in alimentary tract)	Camerano, 1903, 1915
Phoxinus phoxinus (Linnaeus, 1758)	C-Gordionus violaceus (Baird, 1853) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930
Phoxinus phoxinus (Linnaeus, 1758)	G-Gordius aquaticus Linnaeus, 1758 (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Linstow, 1898; Villot, 1891
Phoxinus phoxinus (Linnaeus, 1758)	C-Parachordodes tolosanus (Dujardin, 1842) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Villot, 1891
Phoxinus phoxinus (Linnaeus, 1758)	C-Paragordius stylosus (Linstow, 1883) (cystic stage)	Camerano, 1897a, 1915
Phoxinus phoxinus (Linnaeus, 1758)	C-Paragordius tricuspidatus (Dufour, 1828) (cystic stage)	Blunck, 1922; Camerano, 1915; Dorier, 1930; Villot, 1891

Rhinichthys atratulus atratulus (Hermann, 1804)	C-Paragordius varius (Leidy, 1851) (cystic stage)	Montgomery, 1904
	Order Atheriniformes Family Cyprinodontidae [or Poeciliidae]	
Limia dominicensis (Cuvier and Valenciennes, 1846)	C-Chordodes sp. (developmental stage, in body cavity)	Nigrelli, 1941; 1943
Platypoecilius maculatus Gunther, 1866	C-Chordodes sp. (developmental stage, in body cavity)	Nigrelli, 1941, 1943
Poecilia vivipara Bloch and Schneider, 1801	C-Chordodes sp. (developmental stage, in body cavity)	Nigrelli, 1941, 1943
	Order Gasterosteiformes Family Gasterosteidae	
Gasterosteus aculeatus Linnaeus, 1758	G-Gordius globicola Fabricius, 1780 (? adult stage, in alimentary tract)	Fabricius, 1780; Stiles and Hassall, 1920
	Order Perciformes [=Percomorphi] Family Centrarchidae	
Micropterus punctulatus (Rafinesque, 1819)	C-Chordodes morgani Montgomery, 1898 (developmental stage, in body cavity and sinus venosus)	Nigrelli, 1941, 1943
	Superclass Tetrapoda Class Amphibia Order Anura [=Salientia] Family Bufonidae	
Bufo sp.	G-Gordius sp. (cystic stage)	Blunck, 1922; Dorier, 1930
Bufo sp.	G-Gordius aquaticus Linnaeus, 1758 (cystic stage)	Blunck, 1922; Siebold, 1854

Bufo sp.	C-*Paragordius varius* (Leidy, 1851) (cystic stage)	Montgomery, 1904
Bufo vulgaris Laurenti, 1768	Unstated sp. Gordioidea (? adult stage, in alimentary tract)	Clarke, 1831
	Family Hylidae	
Hyla regilla Baird and Girard, 1852	C-*Neochordodes occidentalis* (Montgomery, 1898) (cystic stage)	Poinar and Doelman, 1974
	Family Ranidae	
Rana clamitans Latreille, 1802	Unstated sp. Gordioidea (? developmental stage)	Flynn, 1973
Rana temporaria Linnaeus, 1758	G-*Gordius* spp. (cystic stage)	Blunck, 1922; Dorier, 1930
Rana temporaria Linnaeus, 1758	G-*Gordius aquaticus* Linnaeus, 1758 (cystic stage; ? developmental stage)	Leydig, 1853; Linstow, 1878; Müller, 1926; Villot, 1884a
Rana temporaria Linnaeus, 1758	Unstated sp. Gordioidea (? adult stage, in alimentary tract)	Clarke, 1831
	Order Caudata [=Urodela] Family Ambystomidae	
Ambystoma mavortium Baird, 1850	G-*Gordius* sp. (? developmental stage, in tissues of forearm)	Garman, 1886
Ambystoma talpoideum (Holbrook, 1838)	Unstated sp. Gordioidea (? developmental stage)	Flynn, 1973

	Family Salamandridae	
Salamandra maculosa Laurenti, 1768 [Salamandra salamandra (Linnaeus, 1758)]	G-Gordius spp. (? cystic stage)	Blunck, 1922; Dorier, 1930
	Class Reptilia Subclass Anapsida Order Chelonia Family Emydidae	
Clemnys capica leprosa (Schweigger, 1812)	G-Gordius aquaticus Linnaeus, 1758 (? adult stage, from alimentary tract)	Sciacchitano, 1962
	Subclass Diapsida Order Squamata Family Lacertidae	
Lacerta vivipara Jacquin, 1787	G-Gordius sp. (? adult stage, from alimentary tract)	Moravec, 1963
	Class Aves Order Galliformes Family Phasianidae	
Gallus gallus (Linnaeus, 1758)	G-? Gordius sp. (? adult stage, in a domestic chicken's egg; ? possibly a nematode)	Gustafson, 1975
	Order Gruiformes Family Otidae	
Chlamydotis undulata macqueenii (Gray, 1832)	C-Paragordius stylosus (Linstow, 1883) (? adult stage; ? possibly recovered from the alimentary tract)	Linstow, 1883b

Class Mammalia
Order Insectivora
Family Erinaceidae

Erinaceus aethiopicus Ehrenberg, 1833	G-*Gordius gialensis* Sciacchitano, 1932 (? adult stage; ? possibly recovered from the alimentary tract)	Sciacchitano, 1932

Order Primates
Family Hominidae

In the following section, a list of associations between gordiids and humans is presented.

Summary and Conclusions

Six hundred and twenty-seven associations between gordiids and lower animals were tabulated in the preceding host list (Table 9).

In general, gordian worms have a wide host range. Five phyla of hosts were shown to be involved: Platyhelminthes with one association, Mollusca with 17, Annelida with 15, Arthropoda with 535, and Chordata with 59.

Stages of Gordioidea associated with non-human hosts were compiled (Tables 10, 11, 12, and 13). The developmental stage had the highest number of associations with 505, followed by the cystic stage with 101, the adult stage with 15, the melanized-nonencysted larval form with 5, and the preparasitic larval form with one. The developmental stage occurred in animals of the Phyla Platyhelminthes, Annelida, Arthropoda, and Chordata. Orders Coleoptera and Orthoptera had 163 and 173 associations, respectively, involving gordiids in the developmental stage.

The range of paratenic hosts included members of the Phyla Mollusca, Annelida, Arthropoda, and Chordata. Twenty-five of the 101 associations, pertaining to the cystic stage of the Gordioidea, involved vertebrates.

The adult stage of gordian worms, as either spurious or accidental parasites, was found to be associated only with chordates, including fishes, amphibians, reptiles, birds, and an insectivore. Many specimens of adult hair-worms were recovered from the alimentary tract.

Genus Gordius had the highest numbers of host associations with 297 in the developmental stage, 41 in the cystic stage, 11 in the adult stage, 4 in the melanized-nonencysted larval form, and one in the preparasitic larval form. Similarly, Genus Gordius had the widest host range which included all 5 previously-mentioned host phyla.

Under certain circumstances, gordiids may play an important role in biological control (refer to introductory remarks in this section), and they possibly could be manipulated by man for use against such insects as grasshoppers and crickets.

SECTION 10

HOST LIST OF THE GORDIOIDEA: NEMATOMORPHA.

II. MAN AS HOST

Introduction

General Considerations

Instances of infection in man by members of the Order Gordioidea, the gordiids, have been documented since medieval times. Various well-known Old World scholars, including Thomas De Cantimpré (*circa* 13th century a, b, and c), Albertus Magnus (1519a and b), and Aldrovandus (1638a and b), have cited in their classic medieval writings the supposed poisonous consequences to man and beasts when hair-worms were inadvertently ingested. A similar belief has been reported by Blanchard (1849) to exist in the New World among the early native populations of Chile. Surprisingly, the morbid fear associated with gordiids has persisted in some quarters of civilization well into the twentieth century (Baylis, 1944).

Understandably, because of errors and confusion in the classification and nomenclature of worm parasites, many early accounts of hair-worms as parasites of man may be questioned.

However, as of the early 1800's, there are still a number of cases which are either most likely genuine or at least highly suspicious as associations of parasitism or pseudoparasitism between gordian worms and man, including instances of the recovery of organisms from feces, urine, and vomitus.

Summaries of previous cases have been prepared by Baylis (1927), Blanchard (1890), Braun (1903, 1908), Braun and Seifert (1925), Brumpt (1949), Camerano (1897a, 1915), Fantham et al. (1920), Faust et al. (1970), Gedoelst (1911), Mattes and Wignand (1958), Railliet (1895), Riddell (1928), Rivas (1920), Stiles (1907), Watson (1960), and others. But even these aforementioned works do not list all known cases because frequently early reports were cited in lesser-known journals or circulated in limited distribution. Some of the more recent reports have also been difficult to retrieve, mainly owing to confusing and variable methods of publication.

I have prepared an updated list of known cases or associations of hair-worms parasitic in man. This list should be useful, as many investigators have expressed divergent and often conflicting viewpoints on the subject. For example, Bacounin (1790), who conducted clinical trials with the gordiids in human subjects, remarked that the worms are easy to swallow. Aside from brief malaise, he and another volunteer suffered no adverse effects. Cobbold (1864) stated, "The medical practitioner would do well to familiarise himself with its appearance, since it is not an uncommon trick with young people to procure the worm for purpose of puzzling the doctor." Brumpt (1949) asserted that accidental parasitism by gordian worms

should only be accepted as a fact when it has been proven by properly-controlled experimentation. On the contrary, the various cases documented by Burger (1972), Carvalho (1942), Faust and Botero Ramos (1960), Foresi and Caroli (1968), Ichihara et al. (1967), León (1914), Parona (1901), Riddell (1928), Singh and Rao (1966), and others substantiate the claim that at least some accounts of hair-worms as parasites of man are indeed genuine. Very recently, Faust et al. (1975) remarked that some published accounts of gordiids considered parasitic in man possibly are fanciful and others erroneous.

Orientation to the Host List

Following is a discussion of the procedure utilized in the preparation of the host list. A rough chronological pattern is used. At the top of each case or association is listed the case number in consecutive order with accompanying date of occurrence in parentheses. Gordian nomenclature is entered in the left-hand column of the list, along with the corresponding names of original authors and dates of first citation for specific species. An abbreviated symbol before the scientific name of the gordiid represents the family of that particular hair-worm. These symbols and their corresponding gordian families, based on the terminology used by Cheng (1973) and Dorier (1965, 1970), are as follows: C=Chordodidae and G=Gordiidae. The right-hand column of the host list gives the reference(s) for the case or association. Below each entry an annotation is provided, often with additional references.

An effort was made to obtain the current valid scientific names for specific gordian species and to update names of places. Doubtful and questionable associations are included to provide as thorough a list as possible. These are so designated to prevent confusion or misinterpretation.

Host List. *Man as Host*

Case 1 (*circa* 13th century)

G-*Gordius* sp. (possibly *G. aquaticus* Linnaeus, 1758) — Thomas De Cantimpré, *circa* 13th century a, b, and c

In his classic "De Natura Rerum," Thomas De Cantimpré pointed out the supposed poisonous nature of ingested *Seta*, which is generally accepted as being equivalent to *Gordius*:

> "Seta vermis est vel potius serpens, ut quidam volunt. A re nomen habet : est enim minimum animal instar sete aut tanquam unus de capillis iube equi. Est autem vermis longus fere cubitalis, gracilis, exilis, ut acus durus et albus et utraque extremitate nichil differens, quippe cui caput non est, sed serpit utrobique cauda. Hic in fontibus, qui torrentibus proveniunt, et in corruptis aquis nec tamen fetidis nascens sepius invenitur. Adeo durus est, ut vix pede conteri possit. Si aquis fervidis imponatur et bulliat, coqui tamen non potest. Veneni eius tanta vis est, ut haustus in potu ab homine elanguere eum faciat atque marcescere, donec eum diro cruciatu vitam exuat. Hoc solo modo infert mortem, alias non."

Speculation exists that some of the account pertained to worms other than hair-worms.

Case 2 (*ante* 1519)

G-*Gordius* sp. (possibly *G. aquaticus* Linnaeus, 1758) — Albertus Magnus, 1519a and b

Albertus Magnus supported the belief that ingested *Seta* causes man to become ill and subsequently die in agony:

"Seta est vermis longus cubitalis adeo exilis ut seta vel pilus de juba vel cauda equi putetur : unde et nomen accepit. Hic in aquis stantibus non multum corruptis generari invenitur, et est adeo durus, quod conteri pede non potest : et si bulliatur, non emollescit. Haustus autem ab homine, cum cruciatu et langore vitam aufert. Aliter autem tactus non infert nocumentum. Hic vermis caput non habere videtur, sed ad utramque partem natat. Forte autem hic de pilis nascitur equorum : quia pili equi in aqua positi stante vitam et spiritum accipiunt, et moventur sicut multoties experti sumus."

It is somewhat doubtful that the supposed poisonous effects are solely due to the presence of gordiids in the alimentary tract.

Case 3 (ante 1638)

G-Gordius sp. (possibly G. aquaticus Linnaeus, 1758) — Aldrovandus, 1638a and b

The Seta or Vitulus aquaticus of Aldrovandus is thought to be a Gordius, possibly G. aquaticus or other species (Cobbold, 1864; Guéguen, 1905a; Rauther, 1930; Riddell, 1928). Aldrovandus affirmed the earlier reports of Thomas De Cantimpré and Albertus Magnus, which mentioned the hair-worms' supposed poisonous effects when swallowed by man or beast.

Case 4 (circa 1771)

G-Gordius sp. [?=Gordius aquaticus Linnaeus, 1758] — Martin, 1771, 1775a and b

Martin reported that humans can become infected with hair-worms by eating parasitized fish. He further stated that fishes acquire their infections while feeding.

The author's claim of a zoonotic process, involving gordiids, fish, and man, was based on equivocal rather than reliable clinical and laboratory diagnoses.

Cases 5, 6 (circa 1790)

?G-Gordius aquaticus Linnaeus, 1758 Bacounin, 1790

Bacounin reported that after feeding gordian worms (presumably G. aquaticus) to animal subjects, such as birds, dogs, and cats, without observing serious ill effects, he then proceeded to swallow two adult worms himself. Except for some brief malaise, the author stated that ingestion was not harmful. He then proceeded to feed six worms to a boy who developed no illness.

Cases 7, 8 (ante 1802)

?G-Gordius aquaticus Linnaeus, 1758 Jördens, 1802

According to Jördens, the Gordius if swallowed would be able to perforate the stomach and intestinal wall with resultant death. He remarked that the Gordius also has the ability to enter skin and to cause inflammation. Bolschwing (1842) is of the opinion that Jördens may have mistakenly confused the guinea worm, a phasmid nematode, for the gordian worm.

Case 9 (1808)

?G-Gordius aquaticus Linnaeus, 1758 Vieweg, 1811

Vieweg presented a report about a female resident from the city of Leningrad (USSR) who was treated for a festering, ulcerous skin lesion. The wound was found to contain hair-worms believed to be G. aquaticus. With topical treatment and a bandage dressing the patient's wound healed.

It is somewhat doubtful, based on the information provided by the author, that this is a confirmed case of gordian parasitism.

Case 10 (*circa* 1821)

C-*Parachordodes tolosanus* (Dujardin, 1842) Degland, 1821, 1823

A gordian specimen, originally identified as *G. aquaticus*, was collected from vomitus of a boy in France. Degland attributed the infection to contaminated potable water. Villot (1884a) redescribed the specimen as *P. tolosanus*.

Case 11 (*circa* 1821)

?C-*Parachordodes tolosanus* (Dujardin, 1842) Degland, 1821, 1823

Degland reported the recovery of a gordiid from the rectum of a French girl who suffered from attacks of colic:

> "M. Martin, medecin distingué de cette ville, m'a assuré qu'une demoiselle de quinze à seize ans fut attaquée l'an dernier, de coliques violentes, et qu'elle rendit par l'anus un ver filiforme, qui ressemblait à celui qui fait l'objet de cette observation."

The author considered the etiology was linked to drinking unsuitable water. Originally, the worm was identified as a specimen of *G. aquaticus*, but it probably should be named *P. tolosanus* instead. [Villot (1884a) redescribed a similar specimen by the latter scientific name; see Case 10.]

Case 12 (*circa* 1822)

Uncertain sp. Cloquet, 1822a, 1822b

A French farmer, who had suffered from attacks of epilepsy, vomited a possible male gordian worm. Cloquet named the recovered

specimen <u>Ophiostoma pouterii</u> and later renamed it <u>O. ponterii</u>. Subsequently, both Blanchard (1890) and Stiles (1907) referred to the specimen as <u>Parachordodes tolosanus</u> (Duj.). However, Riddell (1928) stated it was inappropriate to consider <u>O. ponterii</u> and <u>P. tolosanus</u> as synonyms without the availability of a detailed description of the specimen. I agree with Riddell's position.

Case 13 (<u>ante</u> 1840)

?G-<u>Gordius aquaticus</u> Linnaeus, 1758 Anonymous, 1840

A highly doubtful account is presented on the recovery of <u>G. aquaticus</u> from cutaneous wounds of people in Kurland. The anonymous author stated that hair-worms cause very bad ulcerations of the skin and have to be removed by winding the worms on a small-size stick. Bolschwing (1842) expressed the opinion that the clinical manifestations reported by the anonymous author were indeed caused by the hair-worm and not the guinea worm, <u>Dracunculus medinensis</u>.

Case 14 (<u>ante</u> 1849)

G-<u>Gordius chilensis</u> Blanchard, 1849 Blanchard, 1849

Blanchard documented the belief among the Indian population of Chile that <u>G. chilensis</u> caused severe, grave symptoms if consumed by man from contaminated waters. There is doubt as to the etiology involved, since the species <u>G. chilensis</u> has yet to be adequately described.

Case 15 (1853)

G-*Gordius aquaticus* Linnaeus, 1758 Siebold, 1854

Siebold reported that a 22-year-old German girl vomited a gordian worm after being given an emetic. The author provided a lengthy clinical history of the patient, and he noted that subsequent to expulsion of the hair-worm the girl regained her former good health. The opinion is expressed that possibly the worm was accidentally swallowed by the patient.

Cases 16, 17 (1854)

Unstated sp. Clark, 1854

Clark reported that in 2 separate instances gordiids were passed in urine of women. The voided hair-worms, one from each patient, measured 5 to 6 inches in length.

Case 18 (1854)

Unstated sp. Clark, 1854

Clark briefly stated that a gordiid was coughed up and expelled with sputum. No further details were provided.

Case 19 (*circa* 1854)

Unstated sp. Issacs, 1854

Issacs reported that on various occasions he observed some black-colored animals (possibly gordian worms?) discharged from the skin of his patients. No details were given.

It is presumed that this case and the three cited immediately above occurred somewhere in the United States.

Case 20 (1856)

C-Paragordius varius (Leidy, 1851) Diesing, 1861; Leidy, 1856, 1904

A very brief account is given of the recovery of a male specimen of Paragordius varius, 5 inches in length, from a girl in Ohio. The worm was expelled from the rectum.

Case 21 (1858)

G-Gordius perronciti Camerano, 1897 Heinze, 1937, 1941

Heinze reported the recovery of a gordian worm from vomitus of an Alpine dairy maid in Bavaria. No additional information was provided.

Case 22 (circa 1861)

C-Paragordius varius (Leidy, 1851) Stiles, 1907; White, 1861

White published a note on the recovery in New England of a male specimen of Paragordius varius, 5 inches in length, from a person given aloes. The entry of Stiles, credited to Bowditch of Maine, is probably the same case.

Case 23 (1872)

Uncertain sp. Pepper, 1872

According to Pepper, a male hair-worm of the species Gordius aquaticus was passed by a boy in Texas. No details were given.

It is doubtful that G. aquaticus is the correct name for the specimen, since early American writers frequently identified gordiids of the New World with scientific terminology borrowed from the European literature.

Case 24 (1874)

C-Parachordodes tolosanus (Dujardin, 1842) Camerano, 1888

Camerano stated that he received a female gordian worm from a colleague who found the specimen on an autopsy table:

> "Aggiungero a ciò che precede, che il prof. Pavesi mi spedi esame due esemplari di Gordius che venno trovati a Brescia nel dicembre 1874 sul tavolo di dissezine dell' ospedale presso un cadavere umano."

The case is a doubtful account of host-parasite association between hair-worm and man.

Case 25 (1875)

G-Gordius aquaticus Linnaeus, 1758 Cerruti and Camerano, 1888

Cerruti and Camerano published a report about a 7-year-old Italian youngster who vomited a gordian specimen which was 190 mm. in length. The child had experienced severe gastric pains, but he immediately recovered upon expelling the worm.

Case 26 (circa 1875)

G-Gordius aquaticus Linnaeus, 1758 Patruban, 1875

Before a medical meeting, Patruban displayed a gordian worm, about one-third of a yard in length, which had been passed from the rectum of a child in the region of Dalmatia (Yugoslavia). The author also stated that a second worm had been expelled by the youngster. Patruban suggested the infection may have been acquired when the boy drank water from a stream.

Case 27 (ante 1881)

C-Parachordodes tolosanus (Dujardin, 1842) Fiori, 1881

Fiori reported the rectal passage of a male hair-worm, 183 mm. in length, from a 42-year-old Italian woman. The patient had been given thymic acid for ancylostomiasis. Some hookworms were expelled along with the actively motile gordian worm.

Case 28 (circa 1897)

C-Paragordius tricuspidatus (Dufour, 1828) Blanchard, 1897

After drinking water from a stream, a 15-year-old French boy experienced colic over two weeks' duration. He subsequently removed a thread-like worm from his throat with his fingers, and the symptoms soon subsided. Blanchard identified the specimen as Gordius tricuspidatus. Laboulbène (1897) remarked that the name Filaria tricuspidatus was originally used to designate the involved species.

Case 29 (ante 1898)

? possibly G-Gordius aquaticus Linnaeus, 1758 Linstow, 1898

Linstow mentioned that a gordian specimen in the collection of the Göttingen Museum in Germany had been labeled as follows: " . . . aus einer Frau im Kurland." No further details were given.

It is not clear whether the citation referred to G. aquaticus or another species.

Case 30 (1900)

C-<u>Gordionus</u> <u>violaceus</u> (Baird, 1853) Topsent, 1900

Before a medical meeting, Topsent presented a living male specimen of <u>G.</u> <u>violaceus</u> which had been vomited by a 34-year-old French farmer. The patient had complained of gastric pains for approximately one month, and 8 days prior to expelling the worm, he had a sensation of something moving in his throat. Subsequently, the patient expelled the worm, and his symptoms ceased completely.

Case 31 (<u>circa</u> 1900)

C-<u>Chordodes</u> <u>capensis</u> Camerano, 1895 Baylis, 1927

Baylis identified a gordian specimen that may have been passed possibly <u>per</u> <u>anum</u> by a person from East Africa. No details were provided.

Case 32 (<u>circa</u> 1900)

C-<u>Paragordius</u> <u>varius</u> (Leidy, 1851) Carvalho, 1942

A scant report was made on the passage of a female specimen of <u>P.</u> <u>varius</u> from the rectum of a child in Nebraska. The worm was alive when expelled by the child.

Case 33 (1901)

C-<u>Parachordodes</u> <u>pustulosus</u> (Baird, 1853) Parona, 1901

According to Parona, a specimen of <u>P.</u> <u>pustulosus</u>, 28.5 cm. in length, was passed from the rectum of a 45-year-old Italian woman. The patient experienced rectal discomfort and complained of a moving body within her abdomen. Upon expulsion of the gordiid,

the patient's symptoms of 3 months duration suddenly ceased.

Case 34 (circa 1902)

C-Paragordius varius (Leidy, 1851) Stiles, 1907

Stiles published an account of the rectal passage of P. varius from a 13-year-old Canadian girl. The author remarked that specimens were expelled in large quantities on two separate occasions, a week apart, without the presence of symptoms.

Cases 35, 36 (ante 1903)

Unstated spp. Ward, 1903

Ward noted two episodes which involved the passage of gordian worms from man in Maryland and Michigan respectively. The author considered the expelled worms to be pseudoparasites, but he furnished no details.

Case 37 (1904)

C-Paragordius varius (Leidy, 1851) Stiles, 1907

Stiles cited a brief clinical episode involving the oral passage of two specimens of P. varius from a patient in Illinois.

Case 38 (1905)

C-Gordionus alpestris (Villot, 1884) Guéguen, 1905a and b

Guéguen presented a report with the following clinical background: A 34-year-old Frenchman, who was accustomed to drinking water from an exhausting pump used for draining yards, became afflicted with an attack of colic that lasted two days and then ceased. Some two months later, the man experienced loss of appetite

and vomited for five days. On the fifth day, he vomited a female specimen of G. alpestris, 34.4 cm. in length.

The author suggested that possibly the worm was swallowed when young and developed within the patient's alimentary tract.

Case 39 (ante 1906)

C-Paragordius cinctus Linstow, 1906 Linstow, 1906c

In reviewing the gordian specimens of the Königlichen Zoologichen Museums in Berlin, Linstow reported that a specimen of P. cinctus was recovered from man in the province of Transvaal (South Africa). No additional comments were included.

Case 40 (1908)

Unstated sp. Maxwell, 1908

Maxwell documented the passage of a female gordiid, 13 cm. in length, from the rectum of a 20-month-old child in China. According to the author, the worm was alive when expelled, and the child suffered no ill effects prior to the worm's passage.

Case 41 (circa 1911)

Unstated sp. Herzog, 1913

Herzog cited a possible host-parasite association between man and hair-worm. He reported that a worm was passed from the anus of a Swiss child and that the specimen seemed to resemble the gordian worm described in earlier literature.

Case 42 (*circa* 1912)

G-*Gordius aquaticus* Linnaeus, 1758 Zschokke, 1912a, 1912b; Herzog, 1913

According to Zschokke and later Herzog, a male specimen of *G. aquaticus*, approximately 17 cm. long, and several specimens of *Oxyuris* were passed from the rectum of a young Swiss boy. The child complained of gastric pains and suffered from nervousness and excitability for several weeks prior to expulsion of the worms. Also, a considerable amount of blood was passed from the rectum some weeks before the worms were evacuated.

Zschokke suggested that the child acquired the gordian worm when drinking contaminated water. Riddell (1928) speculated that possibly the gordiid was ingested in the larval form and encysted in the wall of the intestine. Moreover, he conjectured that the appearance of blood in the feces may have been due to the migration of the developing gordian worm back into the lumen of the alimentary tract. Larousse (1967) pointed out that " . . . the larvae (of nematomorphs) are parasitic in aquatic or terrestrial arthropods and also that many other hosts, including frog and even humans, may harbour the encysted larvae."

Case 43 (*circa* 1912)

G-*Gordius aquaticus* Linnaeus, 1758 Léon, (1912) 1914

Two male specimens of *G. aquaticus*, each 20 cm. in length, were reported to have been expelled from the rectum of a 14-year-old Romanian youth, who was treated with cathartics. According to Léon,

the youngster suffered from vague intestinal pains and anal pruritis for about two months prior to the passage of the gordiids. Upon evacuation of the two hair-worms, the child's symptoms regressed. The author considered the symptomatology to be analogous with that seen in infections caused by ascarids.

Case 44 (1927)

G-*Gordius* sp. André, 1927

André presented a brief account of the oral expulsion of a gordian worm from a Swiss girl. The child complained of gastric pains prior to vomiting the worm, but she immediately recovered after ejecting the contents of the stomach.

Case 45 (*circa* 1927)

C-*Paragordius areolatus* Linstow, 1906 Baylis, 1927

Baylis reported that two female gordiids were passed by a West African girl. No details were provided on the route of passage or symptoms involved.

In 1929, Faust briefly referred to a case from S. E. Africa that involved the species *P. areolatus*. It is probable that this latter case may be the same one previously cited by Baylis.

Case 46 (1927)

Undetermined sp. Reardon, 1928

Reardon published a note on the possible but somewhat doubtful passage of a gordian worm from the alimentary tract of a girl in Connecticut. The specimen, originally identified as *Gordius aquaticus*,

was recovered from the toilet bowl after usage by the child. It was suggested that if the worm did not pass from the child's rectum then it may have come into the toilet via the water-service pipes.

Case 47 (1927)

G-Gordius aquaticus Linnaeus, 1758 Riddell, 1928

According to Riddell, a male specimen of G. aquaticus, approximately 13 cm. in length, was passed from the rectum of a one-year-old child in Northern Ireland. The child's mother and nurse both observed the living specimen as they changed the soiled diapers. Riddell added the following interesting remarks, "Because of the age of the patient I have done my best to satisfy myself as to the genuineness of this case, and I do not think there can be any doubt on that point. Both the nurse and mother of the child are exceptionally keen and intelligent, and not to be suspected of any attempt at deception."

Case 48 (1930)

G-Gordius sp. Sandosham, 1953

Sandosham reported that he examined a vial which contained a male gordiid, 31 mm. in length. The vial came from a hospital in Singapore with the following information on the attached label: "Passed per anum by patient at Kampar Hospital, September 1930." The author considered that the information contained on the label was probably correct.

Case 49 (1934)

G-*Gordius robustus* Leidy, 1851 Tanner, 1939

A brief note is presented by Tanner on the passage of *G. robustus* from the urinary tract of a woman in Utah. Tanner stated the attending physician had no doubt that the worm was expelled *per urethram*.

Case 50 (*circa* 1937)

G-*Gordius gesneri* Heinze, 1937 Heinze, 1937, 1941

A male gordian specimen, 78 cm. in length, was vomited by a female patient in a Bavarian hospital. According to Heinze, the patient experienced bouts of nausea and digestive upset prior to expelling the worm. The worm may have been accidentally ingested from contaminated drinking water.

Case 51 (*circa* 1941)

C-*Parachordodes raphaelis* (Camerano, 1893) Craig and Faust, 1943

Faust cited a case which involved the passage of gordiids from the urethra of a young South African girl. He stated that the case was a record from 'Baylis 1941'. However, I was unable to find documentation of the Baylis report in the available scientific literature. Earlier, Yeh and Jordan (1957) remarked that they retrieved data from the British Museum (Natural History) about the specimens concerned. In 1942, the specimens of *P. raphaelis* were presented to the Museum as a gift from de Meillon of the South African Institute of Medical Research.

Case 52 (1942)

C-*Paragordius esavianus* Carvalho, 1942 Carvalho, 1942

Carvalho reported the passage of a living adult specimen of *P. esavianus* from the urinary tract of a Brazilian girl. The author noted that the girl frequently complained of discomfort in the inguinal region and expelled the worm with severe distress. The worm had a length of 211 mm.

Case 53 (*ante* 1943)

? G-*Gordius aquaticus* Linnaeus, 1758 Craig and Faust, 1943; Faust, 1949

Craig and Faust briefly noted the recovery of a gordiid from a human in El Salvador. No description of either the worm parasite or the patient's symptomatology was furnished. However, Faust later stated that the worm was passed in the feces of a 14-year-old school boy. [The identification of the gordiid is questioned by this author.]

Case 54 (*ante* 1944)

C-*Parachordodes wolterstorffii* (Camerano, 1888) Baylis, 1944

In reviewing records on the distribution of hair-worms in the British Isles, Baylis noted one report about a specimen of *P. wolterstorffii* supposedly "passed *per vaginam*" and submitted for examination by a medical man. No further data were available.

It is interesting to point out at this time that Watson (1960) suggested hair-worms may gain entry into the urethra during bathing or washing in pools or quiet streams. Faust *et al*. (1968) proposed that

water used as a vaginal douche may account for urethral discharge of mature gordiids from female subjects.

Case 55 (*ante* 1951)

G-*Gordius* sp. (possibly *G. robustus* Leidy, 1851) — Craig and Faust, 1951

A brief report is made about the recovery of an adult female gordiid from the stool of a 4-year-old child in Missouri.

Case 56 (*ante* 1951)

G-*Gordius* sp. — Craig and Faust, 1951; Mattes and Wignand, 1958

According to Craig and Faust, many immature gordian worms were passed in the urine of a 45-year-old male from South Carolina. The presence of the worms in the urinary tract caused the man to have dysuria. Mattes and Wignand stated that the worms were specimens of *Gordius* sp.

Case 57 (1957)

C-*Pseudogordius tanganyikae* Yeh and Jordan, 1957 — Yeh and Jordan, 1957

A highly interesting episode was documented by Yeh and Jordan. A female specimen of *Pseudogordius tanganyikae*, 172 mm. in length, was passed from either the urethra or the rectum of a 5-year-old girl in East Africa. The child had complaints of vulvovaginitis and lower abdominal pains for some months before passage of the worm. The gordiid was expelled without discomfort in the child's "potty", swimming about in the urine. Upon passage of the worm, the pains in

the child stopped. Examinations of the girl's stools and urine on various occasions failed to detect any pathologic manifestations or clues as to the worm's presence.

Case 58 (1960)

C-Neochordodes columbianus Faust and Botero Ramos, 1960	Faust and Botero Ramos, 1960

Faust and Botero Ramos reported the recovery of two specimens of N. columbianus, one male and one female, from the external meatus of the ear from a girl in Columbia. The two gordiids were 182 and 150 mm. long respectively. According to the authors, movement of the hair-worms in the tissues had caused intense pruritis and the subsequent need for professional medical care.

Case 59 (1961)

G-Gordius inesae Cavalieri, 1961	Cavalieri, 1961; León Varela and Garbarino, 1962

According to Cavalieri, a male specimen of Gordius inesae, 168 mm. in length, was recovered from vomitus of a woman in the Argentine Republic. The association was also described by León Varela and Garbarino.

Case 60 (1961)

C-Chordodes sp.	Fernando and Fernando, 1961

Brief documentation is provided by Fernando and Fernando on the rectal passage of two gordiids, measuring 6 cm. and 16 cm. long respectively, by a 3-year-old child in a hospital in Singapore.

The smaller-sized hair-worm was identified as a member of Chordodes sp.

The authors proposed the following modes of gordian entry into the human body : 1) ingestion of immature gordiids with drinking-water, 2) ingestion of immature gordiids with aquatic vegetation, 3) ingestion of adult or developmental stages already in a host, such as a parasitized insect or other arthropod, and 4) consumption of adult gordiids from contaminated drinking-water.

Case 61 (1962)

C-Chordodes skorikowi Camerano, 1903 — Fernando and Dissanaike, 1962

Fernando and Dissanaike reported the recovery of a male gordiid, 12.3 cm. long, from the vomitus of a 3-year-old girl in Sri Lanka.

Cases 62-67 (1964)

G-Gordius sp. — Foresi and Caroli, 1968

An episode involving at least six confirmed cases of human illness attributed to gordian infection was documented by Foresi and Caroli. According to the authors, several Italian soldiers suddenly became ill and manifested complaints of colic. Fecal samples from six soldiers yielded specimens of Gordius, approximately 4 to 15 cm. in length. Contamination of the domestic water supply by hair-worms was the suspected source of the outbreak.

Case 68 (1966)

G-<u>Gordius</u> <u>reddyi</u> Singh and Rao, 1966 — Singh and Rao, 1966

Singh and Rao reported a highly interesting case of gordian parasitism in man. Four specimens, measuring 23, 28.5, 211, and 266 mm. long respectively, were surgically recovered from a tumorous mass in the orbit of a patient in India. The worms' presence in the orbital tissues undoubtedly influenced the inflammatory-reparative response which resulted in the formation of the tumor.

Case 69 (1966)

G-<u>Gordius</u> sp. — Kagei <u>et</u> <u>al</u>., 1966

Kagei and his co-workers documented the oral expulsion of a female gordian worm by a 5-year-old child in Japan. The case is reviewed by Kamegai (1967).

Case 70 (1967)

G-<u>Gordius</u> sp. — Ichihara <u>et</u> <u>al</u>., 1967

Ichihara and associates reported that a specimen of <u>Gordius</u> sp. was vomited by a 2-year-old Japanese youngster. The child suffered from nausea several times daily for nearly three weeks before expelling the worm. The authors postulated that the youngster acquired the hair-worm by ingesting some item infected with the larvae. Interestingly, Ichihara and colleagues cited Inoue (1962b) who considered the invasion of <u>Gordius</u> into the human body as a kind of migration. The case is reviewed by Kamegai (1967).

Case 71 (<u>circa</u> 1969)

Unstated sp. Maldonado-Moll, 1976

A possible but doubtful case of the passage of hair-worm from a child in Puerto Rico was brought to my attention through personal communication with Dr. Maldonado-Moll. A young and well-to-do woman had recovered a gordian worm from the toilet bowl soon after her child had used the toilet. It was postulated that perhaps the worm was passed from the child's rectum or that the recovered worm had migrated from the outside through the sewer lines and into the toilet bowl.

Case 72 (1972)

C-*Paragordius esavianus* Carvalho, 1942 Burger, 1972

Burger reported the passage of a gordian worm, 15.8 cm. long, from the urethra of a 23-year-old American woman. The author, a specialist in urology, noted that the patient complained of dysuria, frequency in urination, and a feeling of incompletely evacuating the bladder. Excretory urography was normal, but cystoscopy showed that the patient suffered from chronic urethritis and trigonitis. The hair-worm was expelled with slight discomfort. However, the patient subsequently became asymptomatic. Followup cystoscopy was negative. Tests for urinary and fecal parasites were also negative.

It was postulated that the woman acquired the infection possibly by direct migration through the short female urethra while bathing in contaminated waters.

Cases 73-76 (ante 1975)

C-Gordionus sp. Redlich, 1975

In personal communication with Dr. Redlich, I was informed that four specimens of Gordionus sp. in the collection of the University of British Columbia were vomited by small children from the Vancouver area and were forwarded to the University from doctors' offices.

Deleted Case

Dirofilaria conjunctivae (Addario, 1885) Beaver and Orihel, 1965

A case of gordian parasitism originally diagnosed by Sayad et al. (1936) as infection of the orbit by Gordius robustus Leidy has been reexamined and reclassified by Beaver and Orihel as a case of subcutaneous dirofilariasis. The latter workers identified the parasite as D. conjunctivae.

Summary and Conclusions

Seventy-six cases (or associations) involving man and gordiids are presented in the preceding host list. Geographic distribution of the cases was as follows: Europe with 37, North America with 23, Asia with 7, Africa with 5, and South America with 4.

A tabulation of the cases, according to the involved gordian genera and human anatomic sites, was made (Table 14). The majority of cases involved the alimentary tract (53), followed by unstated (or uncertain) anatomic sites (9), urinary tract (8), cutaneous tissues (4), external meatus (1), and orbit (1).

The Genus *Gordius* was implicated in 36 associations, followed by unstated or uncertain genera with 12, *Paragordius* with 10, *Parachordodes* with 7, *Gordionus* with 6, *Chordodes* with 3, and *Neochordodes* and *Pseudogordius* with one each.

The resultant physical and psychological trauma to man attributed to hair-worms is still mysterious, since many of the early reports, and some modern ones, too, are either doubtful or lacking professional verification. On the other hand, valid case histories are documented, and they indicate that gordiids may indeed be parasites or pseudoparasites of man. However, gordian worms are not known to spread any disease.

TABLE 1.--Development of Gordius robustus Leidy from Fertilization to Eclosion (in 68°F Water at pH 6.5)

Day	Observations
0	Fertilization
1	Fertilized eggs fully-differentiated
2	Beginning of 2-cell stage and second cleavage
3-4	Four-cell and 8-cell stage
5	Blastula stage
5-6	Beginning of the formation of mesenchyme
6-8	Formation of mesenchyme
8	Gastrula stage starting (invagination)
10-11	Completion of the gastrula stage
11	Commencement of the formation of the proboscis
15-16	Completion of the larval outline
19-20	Internal organs somewhat discernible
22	Internal organs more differentiated
30	Beginning of eclosion
33	End of eclosion

TABLE 2.--Eclosion of Gordius robustus Leidy under Various Temperature and pH Levels

Group	Approx. Number Organisms	Water Temperature (°F)	Water pH	Days for Eclosion	Estimated Percentage of Eggs Hatched
1	2,000-5,000	68	6.5	30-33	60-75
2	2,000-5,000	50	6.5	60-63	60-75
3	2,000-5,000	39.2	6.5	- -	0
4	2,000-5,000	50 for 15 days, then 68	6.5	40-45	60-65
5	2,000-5,000	39.2 for 15 days, then 68	6.5	40-45	60-65
6	2,000-5,000	68	6.0	30-33	60-70
7	2,000-5,000	50	6.0	60-66	60-70
8	2,000-5,000	39.2	6.0	- -	0
9	2,000-5,000	50 for 15 days, then 68	6.0	40-45	50-60
10	2,000-5,000	39.2 for 15 days, then 68	6.0	40-45	50-55
11	2,000-5,000	68	5.5	30-35	60-65
12	2,000-5,000	50	5.5	50-60	50-60
13	2,000-5,000	39.2	5.5	- -	0
14	2,000-5,000	50 for 15 days, then 68	5.5	40-50	50-55
15	2,000-5,000	39.2 for 15 days, then 68	5.5	40-50	50-60

TABLE 2--Continued

Group	Approx. Number Organisms	Water Temperature (°F)	Water pH	Days for Eclosion	Estimated Percentage of Eggs Hatched
16	2,000-5,000	68	7	- -	0
17	2,000-5,000	50	7	- -	0
18	2,000-5,000	39.2	7	- -	0
19	2,000-5,000	50 for 15 days, then 68	7	- -	0
20	2,000-5,000	39.2 for 15 days, then 68	7	- -	0
21	2,000-5,000	68	7.5	- -	0
22	2,000-5,000	50	7.5	- -	0
23	2,000-5,000	39.2	7.5	- -	0
24	2,000-5,000	50 for 15 days, then 68	7.5	- -	0
25	2,000-5,000	39.2 for 15 days, then 68	7.5	- -	0

TABLE 3.--Early Development of Various Species of the Gordioidea

Species	Time of Oviposition	Time of Eclosion (Maturity to preparasitic larval stage)	Incubation Period (Total days)	Reference
Chordodes japonensis Inoue	May	June	29-30	Inoue, 1958
Gordionus scaber Müller	June 13-15	July 29	About 45	Müller, 1926
Gordius aquaticus Linnaeus			More than one month	Mühldorf, 1914
Gordius robustus Leidy	November-December	December-January	30-33	Present author, in this dissertation
Gordius robustus Leidy	May	May-June	About one month	May, 1919
Neochordodes occidentalis (Montgomery)			Approx. 30	Poinar and Doelman, 1974
Parachordodes tolosanus (Dujardin)	Middle of June	Middle of July	About one month	Meissner, 1856
Paragordius varius (Leidy)			More than 17-19	Montgomery, 1904

TABLE 4.--Effects of Drying upon the Hatchability of Eggs of Gordius robustus Leidy

Egg Strand Number	Approx. Quantity Larvae in Egg Strand	Drying Conditions			Conditions after Replacing Egg Strand in Water		Concluding Observations and Approx. Quantity Eggs Hatched
		Hours	Approx. Moisture (%)	Approx. Temp. (°F)	Approx. Temp. (°F)	pH	
1	500	6	60	68	68	6.5	Hatch; 20-30%
2 (Control)	500	--	--	68	68	6.5	Hatch; 80%
3	500	12	60	68	68	6.5	Hatch; < 10%
4 (Control)	500	--	--	68	68	6.5	Hatch; 80%
5	500	24	60	68	68	6.5	No Hatch
6 (Control)	500	--	--	68	68	6.5	Hatch; 80%
7	500	48	60	68	68	6.5	No Hatch
8 (Control)	500	--	--	68	68	6.5	Hatch; 80%

TABLE 5.--Tolerance of Preparasitic Larvae of *Gordius robustus* Leidy to Drying

Drying Time (Seconds)	Number of Observed Larvae	Time Passed since Water was Added to Surface of Dried Larvae (Minutes)							
		1	1.5	2	2.5	5	15	30	>30
		Number of Larvae that Survived							
5	20	15	15	15	15	15	15	0	0
10	20	15	15	15	15	15	0	0	0
15	20	1	1	1	1	0	0	0	0
20	20	0	0	0	0	0	0	0	0
0 (Controls)	20	20	20	20	20	20	20	20	20

TABLE 6.--Field Survey of Invertebrate and Vertebrate Animals*
for Hosts of Gordius robustus Leidy

Animals Collected and Examined (Quantity)	Observations
A. Phylum Mollusca	
1. Snails	
Helix aspersa Müller (500)	No gordiids observed
2. Slugs	
Deroceras laevae (Müller)(425)	" " "
Deroceras reticulatum(Müller)(200)	" " "
Limax maximus Linnaeus (5)	" " "
B. Phylum Annelida	
1. Earthworms	
Eisenia sp. (110)	" " "
2. Unidentified fresh-water leeches(5)	" " "
C. Phylum Arthropoda	
1. Spiders	
Order Araneida (2)	" " "
2. Field crickets	
Gryllus sp. (15)	" " "
3. Water striders	
Gerris sp. (45)	" " "
4. Mosquitoes	
Culex spp. - larvae (500)	" " "
Culex tarsalis Coquillett (7)	" " "
5. Honeybees	
Apis mellifera Linnaeus (4)	" " "
6. Bumblebees	
Bombus sp. (2)	" " "
7. Earwigs	
Order Dermaptera (6)	" " "

TABLE 6--Continued

Animals Collected and Examined (Quantity)	Observations
8. Dragonflies Order Odonata-adults (15) and their aquatic nymphs (25)	No gordiids observed
9. Damselflies Order Odonata - adults (1) and their aquatic nymphs (15)	Three gordian larvae noticed in the lumen of the alimentary tract of an aquatic nymph
10. Sowbugs *Porcello* sp. (100)	No gordiids observed
11. Jerusalem crickets *Stenopelmatus longispina* Brunner (2)	Two adolescent gordiids recovered, one from each cricket
12. Mayflies Order Ephemeroptera- aquatic nymphs (6)	No gordiids observed
13. Beetles (various families)	
Carabidae (3)	" " "
Coccinellidae (4)	" " "
Dytiscidae (3)	" " "
Hydrophilidae (1)	" " "
Tenebrionidae (7)	" " "
14. Ants *Monomorium* sp. (12)	" " "
15. Termites Order Isoptera (2)	" " "
16. Tabanid flies *Tabanus* sp. - larvae (37)	" " "
17. Caddisflies Order Tricoptera - larvae (5)	" " "
18. Midges Family Chironomidae (5)	" " "
19. Black flies *Simulium* sp. (3)	" " "

TABLE 6--Continued

Animals Collected and Examined (Quantity)	Observations
20. Moth flies Family Psychodidae (2)	No gordiids observed
21. House flies *Musca domestica* Linnaeus (4)	" " "
22. Little house flies *Fannia canicularis* (Linnaeus) (2)	" " "
23. Paper wasps *Polistes* sp. (10)	" " "
24. Unidentified lepidopterous larvae (18)	" " "
25. Monarch butterfly *Danaus plexippus* (Linnaeus) (1)	" " "
D. Phylum Chordata	
1. Top-water minnows *Gambusia affinis* (Baird and Girard) (26)	" " "
2. Frogs *Hyla regilla* Baird and Girard--adults (6) and tadpoles (105)	" " "
Rana sp. (1)	" " "
3. Toads *Bufo* sp. (1)	" " "
4. California slender salamanders *Batrachoseps attenuatus* (Eschscholtz) (47)	" " "
5. Sagebrush lizards *Sceloporus graciosus* Baird and Girard (3)	" " "

TABLE 6--Continued

Animals Collected and Examined (Quantity)	Observations
6. Sparrows _Passer_ sp. (2)	No gordiids observed
7. House mouse _Mus musculus_ Linnaeus (1)	" " "

* The above animals were collected at sites in Northern California where adult specimens of _G. robustus_ had been recovered.

TABLE 7.--Gordian Worms in American Potable Water Supplies and Related Distribution Systems

Health Jurisdiction	Remarks from Available Data
Alabama	No record
Alaska	No record
Arizona	Approximately 4 to 6 specimens submitted each year; often in water of toilet bowls.
Arkansas	Found from time to time in water supplies.
California	Occasionally found in potable water supplies and plumbing fixtures, such as sinks, bath tubs, and toilet bowls.
Colorado	A few specimens collected over the past 15 years from potable water supplies.
Connecticut	No record
Delaware	No record
Florida	No record
Georgia	No record
Hawaii	No record
Idaho	No record
Illinois	No record
Indiana	No record
Iowa	Occasionally reported from water samples submitted to the State Hygienic Laboratory for examination.
Kansas	One specimen collected from a water sample.
Kentucky	No record
Louisiana	No record

TABLE 7--Continued

Health Jurisdiction	Remarks from Available Data
Maine	No record
Maryland	No record
Massachusetts	No record
Michigan	No record
Minnesota	No record
Mississippi	Recovered from time to time from potable water supplies; coincides with periods of heavy cricket infestation and the presence of a ground reservoir or aerator in which the screening was found to be defective; occasionally closed system exceptions have been traced to wells where the screen had been lost from the vent.
Missouri	No record
Montana	In 10 years, six episodes of gordian worms in water supplies, including one account of a gordiid found in a toilet bowl.
Nebraska	No record
Nevada	No record
New Hampshire	No record
New Jersey	No record
New Mexico	No record
New York	No record
North Carolina	No record
North Dakota	A considerable number of specimens submitted each year to the State Public Health Laboratory; specimens are usually associated with infant diapers (insect contamination) and water in toilet bowls; one specimen possibly recovered from a distribution system.

TABLE 7--Continued

Health Jurisdiction	Remarks from Available Data
Ohio	A few specimens but no details on the circumstances of their recovery.
Oklahoma	No record
Oregon	Collected from time to time from toilets using well water.
Pennsylvania	No record
Rhode Island	No record
South Carolina	A gordian worm is seen approximately every two years.
South Dakota	Very occasionally recovered from potable water supplies.
Tennessee	No record
Texas	Twenty-five specimens recovered between 1965 and mid-1975 from sinks, toilet bowls, and other fixtures.
Utah	One specimen recovered from a kitchen sink; information on another specimen is lacking.
Vermont	No record
Virginia	About once a year, water samples are received which have gordian worms in them.
Washington	No record
West Virginia	No record
Wisconsin	No record
Wyoming	No record

TABLE 7--Continued

Health Jurisdiction	Remarks from Available Data
American Samoa	No record
District of Columbia	No record
Guam	No record
Panama Canal Zone	No record
Puerto Rico	No record
Trust Territory of the Pacific Islands	No record
Virgin Islands	No record

TABLE 8.--Effects of Various Chemical Disinfectants on *Gordius robustus* Leidy (at Average Aquatic pH 6.5 and Temperature 68°F)

	Number of Worms	Chlorine or Iodine (ppm.) Initial Total	Residual Total	Contact time (min.)	Observations
Halazone-2 tablets	5 adults	4	3.4	30	One sluggish
	Approx. 50 larvae	4	3.4	30	Moderate infection in body cavity of mosquito larvae
Halazone-4 tablets	5 adults	8.1	6.2	30	Four killed + 1 stunned
	Approx. 50 larvae	8.1	6.2	30	No infection of mosquito larvae
Chlorine soln. from sodium hypochlorite	5 adults	1.8	1.2	30	All 5 actively motile
	Approx. 50 larvae	1.8	1.2	30	Heavy infection in body cavity of mosquito larvae
Chlorine soln. from sodium hypochlorite	5 adults	5.5	4.8	30	Two killed + 1 stunned (but later died)
	Approx. 50 larvae	5.5	4.8	30	No infection of mosquito larvae
Chlorine soln. from sodium hypochlorite	5 adults	19.6	17.8	30	All 5 killed
	Approx. 50 larvae	19.6	17.8	30	No infection of mosquito larvae
Iodine soln. from crystalline iodine	5 adults	Approx. 4	Approx. 4	30	Three killed + 2 stunned
	Approx. 50 larvae	Approx. 4	Approx. 4	30	No infection of mosquito larvae
Control--no treatment	5 adults	0.0	0.0	30	All 5 actively motile
	Approx. 50 larvae	0.0	0.0	30	Heavy infection in body cavity of mosquito larvae

TABLE 9.--Principal Groups of Host Animals (Other than Man) Associated with the Gordioidea (Arranged According to the Involved Stage(s) in the Gordian Life Cycle)

Principal Groups of Host Animals (Other than Man)	Total Associations Between Gordiids and Various Hosts	Stages of Gordioidea in Host Animals (Other than Man)				
		Cystic	Preparasitic Larval Forms	Melanized-Nonencysted	Developmental	Adult
Totals:	627	101	1*	5	505	15
Phylum Platyhelminthes	1				1	
Class Trematoda	1				1	
Order Digenea	1				1	
Phylum Mollusca	17	17				
Class Gastropoda	17	17				
Order Stylommatophora	3	3				
Order Basommatophora	14	14				
Phylum Annelida	15	12			3	
Class Oligochaeta	8	8				
Order Plesiopora	5	5				
Order Prosopora	2	2				
Order Opisthopora	1	1				
Class Hirudinea	7	4			3	
Order Rhynchobdellida	1				1	
Order Pharyngobdellida	6	4			2	
Phylum Arthropoda	535	47	1*	5	482	
Class Arachnida	13				13	
Order Scorpionida	1				1	
Order Araneae	12				12	
Class Crustacea	5	3			2	
Order Notostraca	1				1	
Order Podoplea	1	1				
Order Isopoda	1	1				
Order Amphipoda	1	1				
Order Podophthalmia	1				1	
Class Insecta	506	44	1*	5	456	
Order Thysanura	6	4			2	
Order Odonata	7		1*		6	
Order Ephemeroptera	12	5			7	
Order Orthoptera	173				173	
Order Dermaptera	6				6	
Order Plecoptera	1	1				
Order Hemiptera	4				4	
Order Homoptera	5				5	
Order Neuroptera	2	1			1	
Order Trichoptera	19	6			13	
Order Lepidoptera	57				57	
Order Diptera	33	23		5	5	
Order Coleoptera	167	4			163	
Order Hymenoptera	14				14	
Class Chilopoda	3				3	
Order Lithobiomorpha	1				1	
Order Scolopendromorpha	2				2	
Class Diplopoda	8				8	
Order Glomerida	2				2	
Order Polydesmida	1				1	
Order Spirobolida	1				1	
Order Julida	4				4	
Phylum Chordata	59	25			19	15
Class Cyclostomata	6	5			1	
Order Petromyzontiformes	6	5			1	
Superclass Pisces (class unstated)	1					1
Class Osteichthyes	34	13			14	7
Order Clupeiformes	1					1
Order Salmoniformes	8	1			6	1
Order Isospondyli	1					1
Order Heterognathi	1				1	
Order Ostariophysi	18	12			3	3
Order Atheriniformes	3				3	
Order Gasterosteiformes	1					1
Order Perciformes	1				1	
Class Amphibia	13	7			4	2
Order Anura	10	6			2	2
Order Caudata	3	1			2	
Class Reptilia	2					2
Order Chelonia	1					1
Order Squamata	1					1
Class Aves	2					2
Order Galliformes	1					1
Order Gruiformes	1					1
Class Mammalia	1					1
Order Insectivora	1					1

*Preparasitic gordian larvae found in the alimentary tract of an aquatic damselfly nymph.

TABLE 10.--Distribution of the Cystic Stage of Members of the Gordioidea in Host Animals (Other than Man)

Principal Groups of Host Animals (Other than Man)	Genera of Gordian Worms						Total Associations Between Gordiids and Various Hosts
	Chordodes	Gordionus	Gordius	Neochordodes	Parachordodes	Paragordius	
Totals:	3	10	41	2	23	22	101
Phylum Mollusca		2	10		3	2	17
Class Gastropoda		2	10		3	2	17
Order Stylommatophora			3				3
Order Basommatophora		2	7		3	2	14
Phylum Annelida		1	5		3	3	12
Class Oligochaeta			4		2	2	8
Order Plesiopora			3		2		5
Order Prosopora			1			1	2
Order Opisthopora						1	1
Class Hirudinea		1	1		1	1	4
Order Pharyngobdellida		1	1		1	1	4
Phylum Arthropoda	3	4	16	1	14	9	47
Class Crustacea					1	2	3
Order Podoplea					1		1
Order Isopoda						1	1
Order Amphipoda						1	1
Class Insecta	3	4	16	1	13	7	44
Order Thysanura			2			2	4
Order Ephemeroptera	1		2		2		5
Order Plecoptera			1				1
Order Neuroptera					1		1
Order Trichoptera			4		2		6
Order Diptera	2	3	6	1	7	4	23
Order Coleoptera		1	1		1	1	4
Phylum Chordata		3	10	1	3	8	25
Class Cyclostomata		1	1		1	2	5
Order Petromyzontiformes		1	1		1	2	5
Class Osteichthyes		2	4		2	5	13
Order Salmoniformes			1				1
Order Ostariophysi		2	3		2	5	12
Class Amphibia			5	1		1	7
Order Anura			4	1		1	6
Order Caudata			1				1

TABLE 11.--Distribution of Preparasitic* and Melanized-Nonencysted Larval Forms of Members of the Gordioidea in Host Animals (Other than Man)

Principal Groups of Host Animals (Other than Man)	Genera of Gordian Worms: Gordius	Genera of Gordian Worms: Neochordodes	Total Associations Between Gordiids and Various Hosts
Totals:	5	1	6
Phylum Arthropoda	5	1	6
Class Insecta	5	1	6
Order Odonata	1*		1*
Order Diptera	4	1	5

*Preparasitic gordian larvae found in the alimentary tract of an aquatic damselfly nymph.

TABLE 12.--Distribution of the Developmental Stage of Members of the Gordioidea in Host Animals (Other than Man)

Principal Groups of Host Animals (Other than Man)	Genera of Gordian Worms														Total Associations Between Gordiids and Various Hosts
	Acutogordius	Beatogordius	Chordodes	Chordodiolus	Dacochordodes	Euchordodes	Gordionus	Gordius	Neochordodes	Parachordodes	Paragordionus	Paragordius	Pseudochordodes	Unstated	
Totals:	1	4	65	1	1	1	30	297	6	56	1	22	1	19	505
Phylum Platyhelminthes								1							1
Class Trematoda								1							1
Order Digenea								1							1
Phylum Annelida								3							3
Class Hirudinea								3							3
Order Rhynchobdellida								1							1
Order Pharyngobdellida								2							2
Phylum Arthropoda	1	4	58	1	1	1	30	283	6	56	1	22	1	17	482
Class Arachnida		1						9	1	1				1	13
Order Scorpionida														1	1
Order Araneae		1						9	1	1					12
Class Crustacea								2							2
Order Notostraca								1							1
Order Podophthalmia								1							1
Class Insecta	1	3	58	1	1	1	28	266	5	55	1	22	1	13	456
Order Thysanura								1				1			2
Order Odonata						1		4		1					6
Order Ephemeroptera								2		1		4			7
Order Orthoptera	1	3	58	1			2	88	4			11	1	4	173
Order Dermaptera							1	3	1	1					6
Order Hemiptera								3				1			4
Order Homoptera								5							5
Order Neuroptera								1							1
Order Trichoptera								10		2		1			13
Order Lepidoptera								52		3				2	57
Order Diptera								4				1			5
Order Coleoptera					1		25	79		47	1	3		7	163
Order Hymenoptera								14							14
Class Chilopoda								3							3
Order Lithobiomorpha								1							1
Order Scolopendromorpha								2							2
Class Diplopoda							2	3						3	8
Order Glomerida								2							2
Order Polydesmida							1								1
Order Spirobolida								1							1
Order Julida							1							3	4
Phylum Chordata			7					10						2	19
Class Cyclostomata								1							1
Order Petromyzontiformes								1							1
Class Osteichthyes			7					7							14
Order Salmoniformes			2					4							6
Order Heterognathi			1												1
Order Ostariophysi								3							3
Order Atheriniformes			3												3
Order Perciformes			1												1
Class Amphibia								2						2	4
Order Anura								1						1	2
Order Caudata								1						1	2

TABLE 13.--Distribution of the Adult Stage of Members of the Gordioidea in Host Animals (Other than Man)

Principal Groups of Host Animals (Other than Man)	Genera of Gordian Worms			Total Associations Between Gordiids and Various Hosts
	Gordius	Paragordius	Unstated	
Totals:	11	1	3	15
Phylum Chordata	11	1	3	15
Superclass Pisces (class unstated)			1	1
Class Osteichthyes	7			7
Order Clupeiformes	1			1
Order Salmoniformes	1			1
Order Isospondyli	1			1
Order Ostariophysi	3			3
Order Gasterosteiformes	1			1
Class Amphibia			2	2
Order Anura			2	2
Class Reptilia	2			2
Order Chelonia	1			1
Order Squamata	1			1
Class Aves	1	1		2
Order Galliformes	1			1
Order Gruiformes		1		1
Class Mammalia	1			1
Order Insectivora	1			1

TABLE 14.--Summary of Associations (Cases) between Members of the Gordioidea and Man (Arranged According to the Involved Gordian Genera and Human Anatomic Sites)

Gordian Genera	Human Anatomic Sites						Total Associations
	Alimentary Tract	Cutaneous Tissues	External Meatus	Orbit	Urinary Tract	Unstated or Uncertain	
Chordodes	3						3
Gordionus	6						6
Gordius	29	3		1	2	1	36
Neochordodes			1				1
Parachordodes	4				2	1	7
Paragordius	6				2	2	10
Pseudogordius						1	1
Unstated or Uncertain	5	1			2	4	12
Total Associations	53	4	1	1	8	9	76

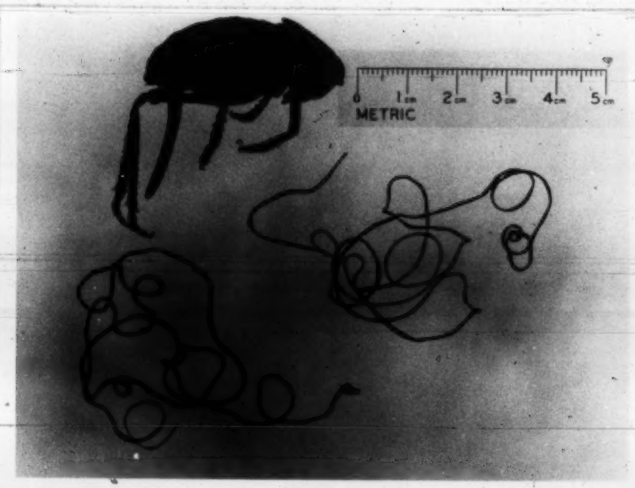

Fig. 1. Juvenile forms of Gordius robustus recovered from the hemocoel of an orthopteran host, Anabrus simplex. Specimens furnished by Dr. C. G. Alexander.

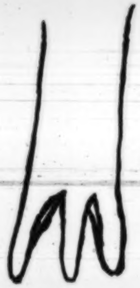

Fig. 2. Posterior extremity of a female specimen of Paragordius varius, surface view. Approx. 50X.

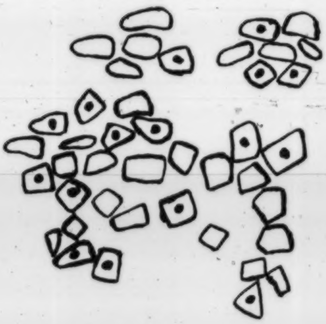

Fig. 3. Surface view of areolae of female Paragordius varius. Approx. 950X.

Fig. 4. Posterior end of male of Gordius robustus, ventral view. Approx. 40X.

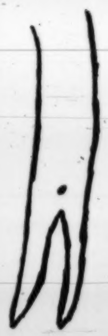

Fig. 5. Posterior extremity of male of Paragordius varius, ventral view. Approx. 50X.

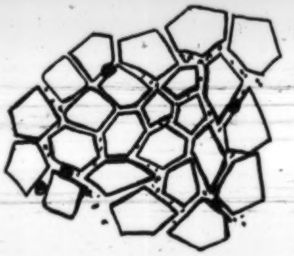

Fig. 6. Areolae of male Gordionus alpestris (adapted from Dorier, 1930, and Heinze, 1937).

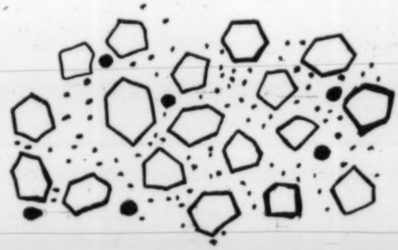

Fig. 7. Areolae of male Gordionus violaceus (adapted from Dorier, 1930, and Heinze, 1937).

Fig. 8. Posterior terminal of a male specimen of Gordionus densareolatus, ventral view (adapted from Montgomery, 1898a).

Fig. 9. Broad surface view of the areolae of male Gordionus densareolatus, with arrow denoting the line of the longitudinal axis of the body (prepared from descriptions in Montgomery, 1898a and b).

Fig. 10. Posterior extremity of male Gordionus longareolatus, ventral view (adapted from Montgomery, 1898b).

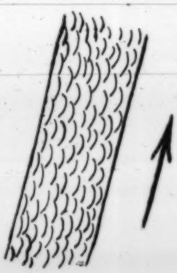

Fig. 11. Broad surface view of Gordionus longareolatus, with arrow depicting the line of the longitudinal axis of the body (adapted from Montgomery, 1898b).

Fig. 12. Posterior terminal of female Gordius robustus, oblique view. Approx. 40X.

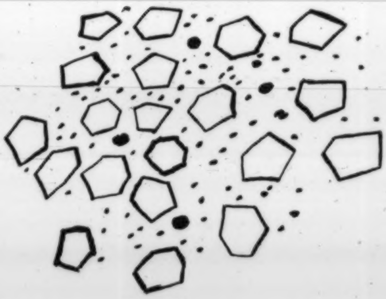

Fig. 13. Areolae of female specimen of Gordionus violaceus. Approx. 950X.

Fig. 14. Surface areolae of female Gordionus densareolatus (adapted from Montgomery, 1898a).

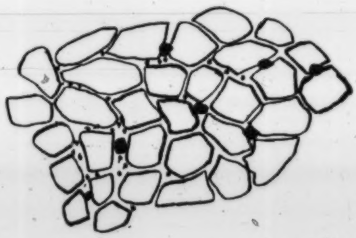

Fig. 15. Areolae of female Gordionus alpestris. Approx. 950X.

Fig. 16. Posterior end of a male specimen of Neochordodes occidentalis. Approx. 40X.

Fig. 17. Posterior extremity of female Neochordodes occidentalis. Approx. 40X.

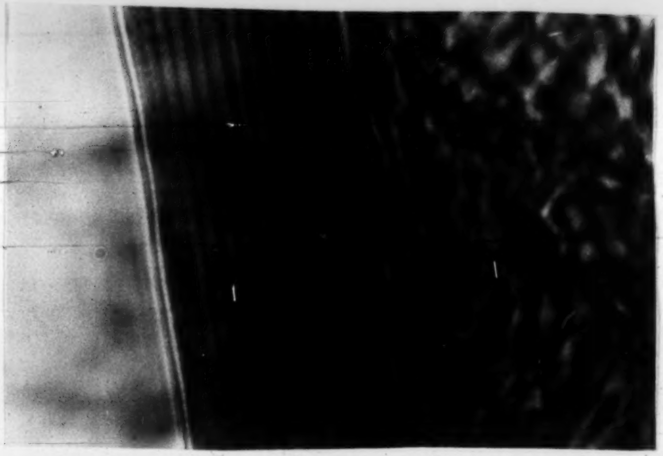

Fig. 18. Gordius robustus, transverse section of body wall. Note cuticular surface lacks areolae. Approx. 375X.

Fig. 19. Surface view of cuticle of Gordius robustus; shows light-colored spots (s) and cuticular fibers (cf). Approx. 650X.

Fig. 20. Anterior extremity of a male Gordius robustus showing the rudimentary oral aperture (arrow). Approx. 70X.

Fig. 21. A female specimen of Gordius robustus displaying a rudimentary mouth (arrow). Approx. 95X.

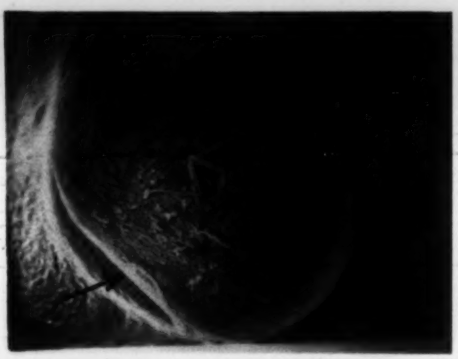

Fig. 22. The posterior end of a female Gordius robustus with the cloacal opening, hidden from view, in the slightly-grooved, truncated area (arrow). Approx. 70X.

Fig. 23. The posterior extremity of a male Gordius robustus showing distinct bilobed prongs. Approx. 95X.

Fig. 24. A male specimen of Gordius robustus showing the slightly-flattened appearance on the inner side of the conical-shaped lobes. Approx. 60X.

Fig. 25. A male Gordius robustus exhibiting on its ventral surface, anterior to the caudal lobes, a crescent-shaped ridge (R). Immediately anterior to the middle of the ridge is the cloacal aperture (C). Approx. 80X.

Fig. 26. A site of collection of Gordius robustus in Contra Costa County, California.

Fig. 27. Another location in Contra Costa County, California, where adults of Gordius robustus were collected.

Fig. 28. Spermatozoa of Gordius robustus collected from the anterior cloaca of a copulating female specimen; phase contrast view; head (h), tail (t). Approx. 3,200X.

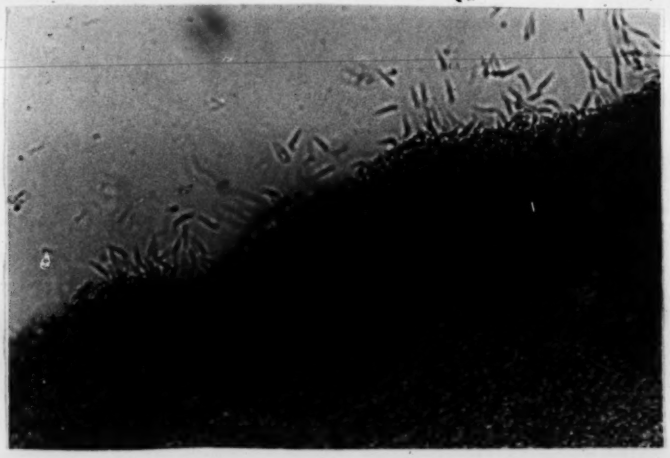

Fig. 29. Spermatozoa of Gordius robustus fertilizing an egg mass (recovered from the antral chamber of a female worm about one hour after the onset of copulation). Approx. 400X.

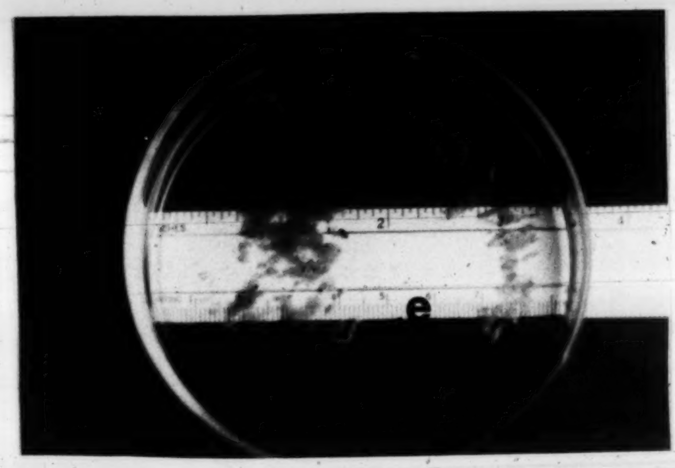

Fig. 30. Egg strands (e) of Gordius robustus collected over a 7-day period. Note that fungi contaminate the water.

Fig. 31. Fertilized eggs of Gordius robustus on day 1. Approx. 650X.

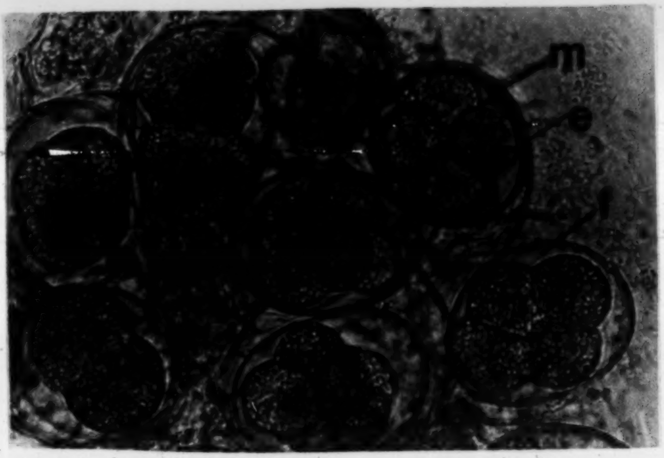

Fig. 32. Two-cell (t), 4-cell (f), and 8-cell (e) stages of Gordius robustus. An egg membrane (m) surrounds the dividing cells. Approx. 650X.

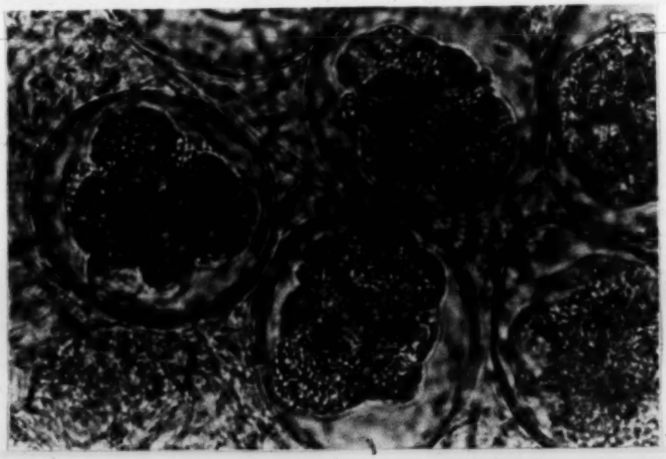

Fig. 33. Gordius robustus. Blastula stage. Approx. 650X.

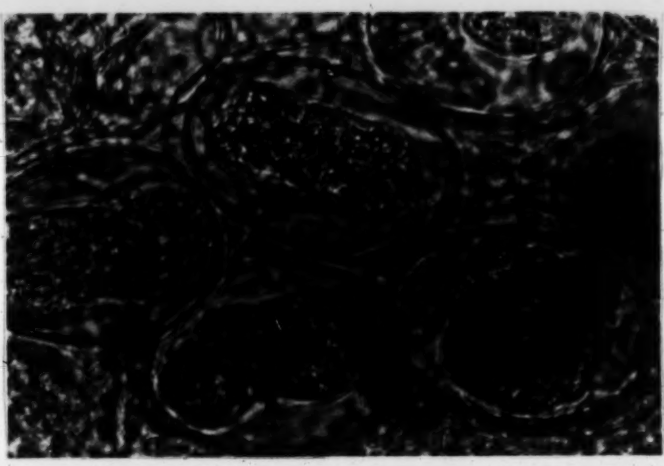

Fig. 34. Gordius robustus. Beginning of gastrulation with characteristic invagination (arrow). Approx. 650X.

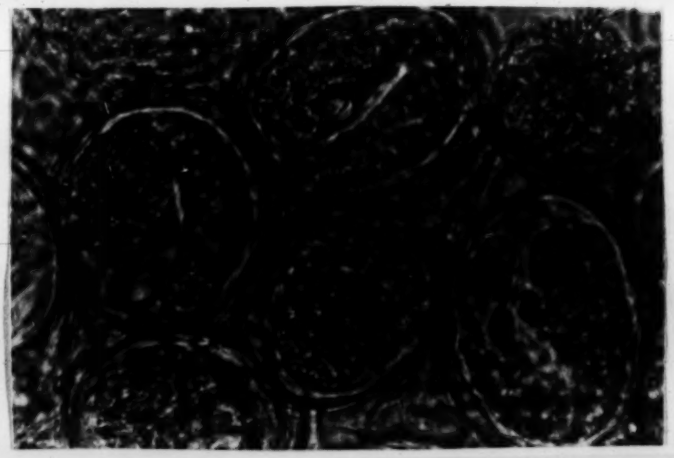

Fig. 35. Gordius robustus. Gastrula stage completed. Approx. 650X.

Fig. 36. Larvae of Gordius robustus undergoing development inside egg shells. Note the proboscis (p). Approx. 650X.

Fig. 37. Preparasitic larvae of Gordius robustus hatching from egg shells; some larvae have their proboscis extended. Note egg mass (m) at the left-hand edge of the figure. Approx. 375X.

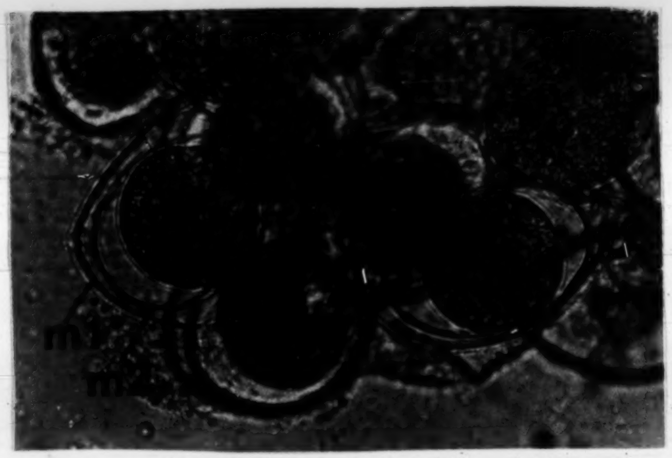

Fig. 38. Gordius robustus. Egg mass showing two separate membranes around individual eggs (m1 and m2). Approx. 650X.

Fig. 39. Immature stages of Gordius robustus. Note outer and inner membranes (m1 and m2) around eggs. The outer membranes link adjacent eggs. Approx. 650X.

Fig. 40. Adult specimen of Gordius robustus. Approx. 0.5X.

Fig. 41. Recently-hatched preparasitic larva of Gordius robustus. Approx. 650X.

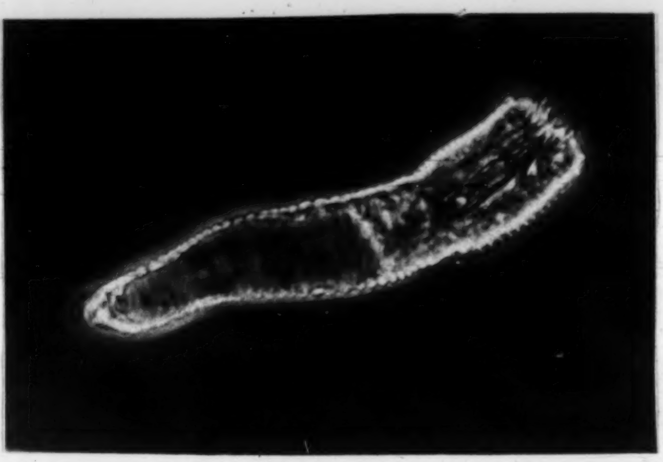

Fig. 42. Recently-hatched preparasitic larva of Gordius robustus; phase contrast view. Approx. 650X.

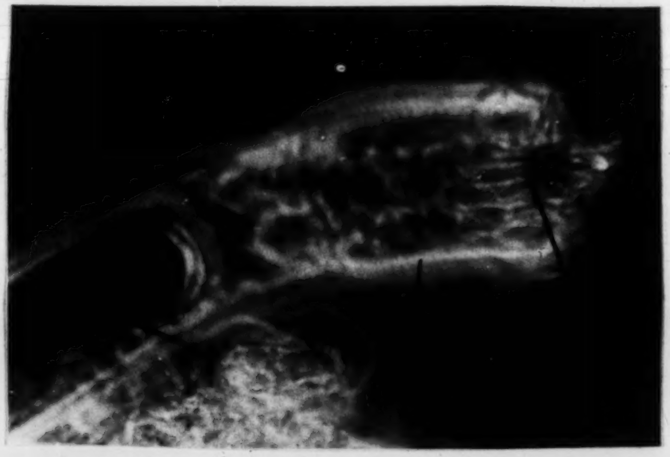

Fig. 43. Preparasitic larva of Gordius robustus in phase contrast view. Note preseptum (pr), anterior portion of pseudo-intestine (i), proboscis (p), and retractile stylets (rs). Approx. 875X.

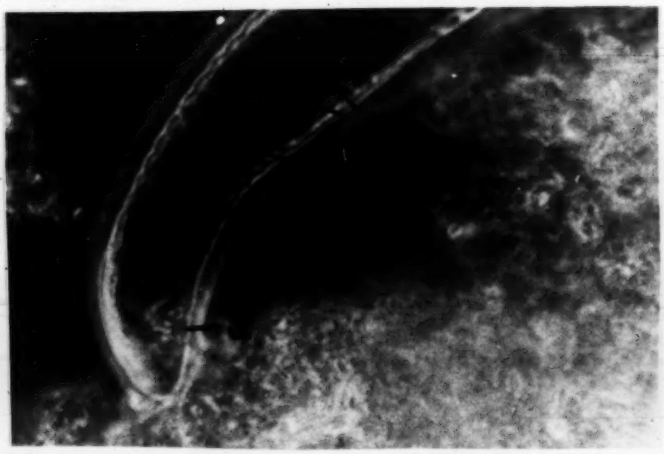

Fig. 44. Preparasitic larva of Gordius robustus in phase contrast view. Note postseptum (ps), pseudointestine (i), globules (g), and anal orifice (a). Approx. 875X.

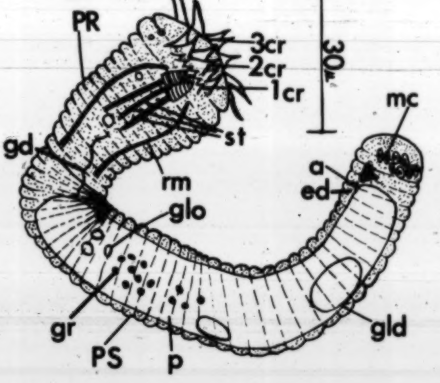

Fig. 45. Preparasitic larva of Gordius robustus in lateral view. PR, preseptum; PS, postseptum; st, retractile stylets; 1cr, first circlet of hooklets; 2cr, second circlet of hooklets; 3cr, third circlet of hooklets; rm, retractor muscles; gd, gland duct; p, pseudointestine or intestinal sac; gr, granules; glo, globules; gld, gland; ed, excretory duct; a, anal aperture; mc, mesenchymal cells. Drawn with the aid of the camera lucida.

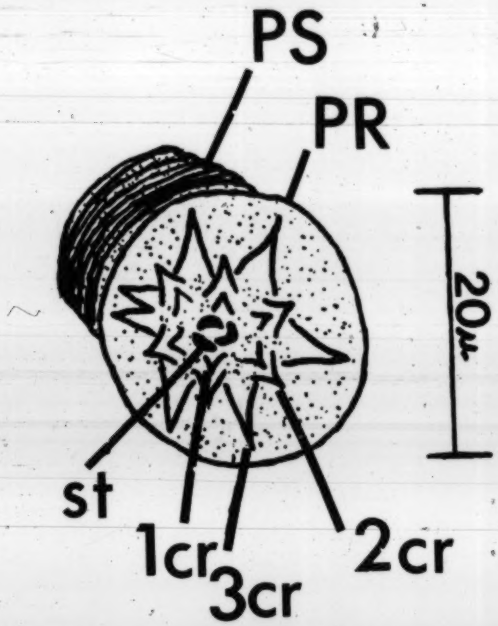

Fig. 46. Apical view of preparasitic larva of Gordius robustus. PR, preseptum; PS, postseptum; st, retractile stylets; 1cr, first circlet of hooklets; 2cr, second circlet of hooklets; 3cr, third circlet of hooklets. Drawn with the aid of the camera lucida.

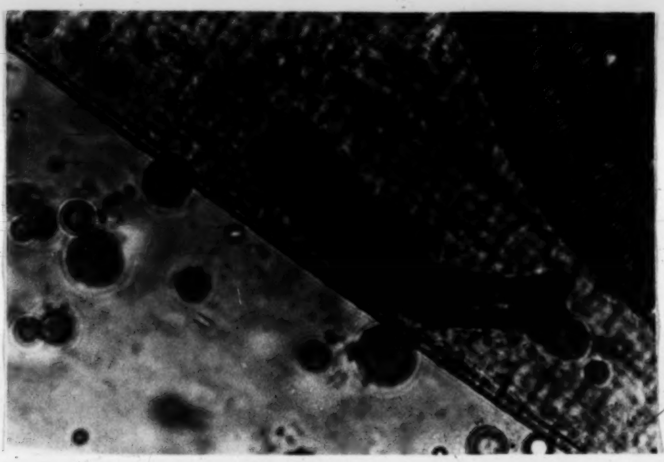

Fig. 47. A larva of Gordius robustus encased in melanin in a 4th-stage larva of Culex pipiens. Approx. 450X.

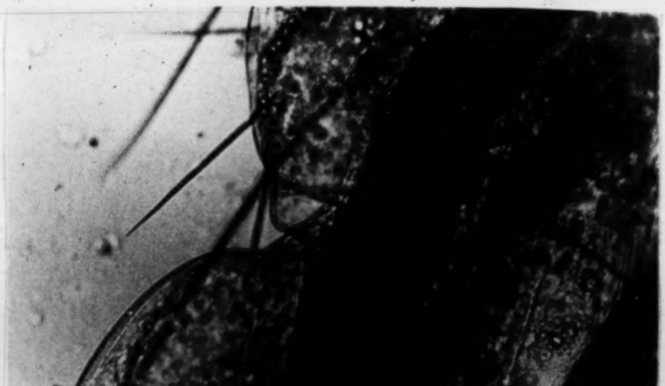

Fig. 48. A melanized larva of Gordius robustus in a 4th-stage larva of Culex tarsalis. Approx. 250X.

Fig. 49. Preparasitic gordian larva, presumably Gordius robustus, recovered from the lumen of the alimentary tract of an aquatic damselfly nymph. Approx. 450X.

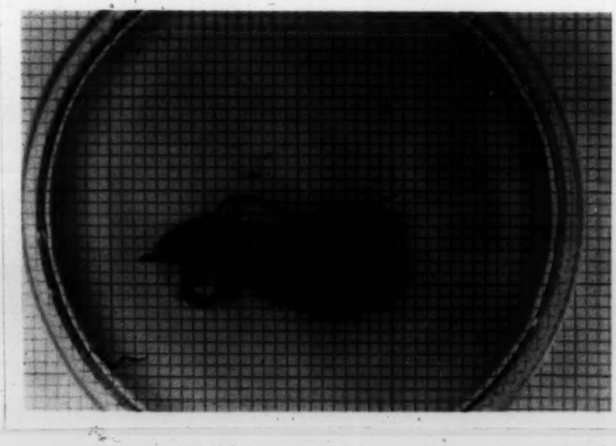

Fig. 50. Adolescent specimen of Gordius robustus recovered from Stenopelmatus longispina.

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